The Systematics and Some Aspects of the Ecology of the Genus *Dendronotus*

(Gastropoda : Nudibranchia)

BY

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(Plates 63 and 64; 28 Text figures)

INTRODUCTION

The genus *Dendronotus* has had a long and chaotic literary history, beginning in 1774 when Ascanius described the type species under the name of *Amphitrite frondosa.* Müller (1776) incorporated this species into his rather all-inclusive genus *Doris* as *Doris arborescens.* Cuvier (1797) established the genus *Tritonia* and he included *A. frondosa* as *Tritonia arborescens* in 1817. Alder & Hancock (1845), on morphological bases, established the genus *Dendronotus* as separate from *Tritonia* with *Doris arborescens* Müller, 1776 as the type species. Subsequently, the genus has been referred to as *Dendronotus* with the name of the type species *D. frondosus* (Ascanius, 1774) being used for the first time in the 1904 edition of the Plymouth Marine Invertebrate Fauna (Eliot, 1910).

During the late 18th, 19th and early 20th centuries, the species of *Dendronotus,* especially *D. frondosus,* were, with only a few exceptions (Alder & Hancock, 1845; Verrill, 1870; MacFarland, 1966), based on sketchy, inadequate descriptions and diagrams of one or a few animals. Consequently, there are no reports on the range of intraspecific variation of the various taxonomically important characters, the radula excluded, for any species.

Odhner (1934), in an effort to point out some of the pitfalls facing opisthobranch taxonomists and what they might do to avoid the same, states:

> "... I think it is necessary to give good figures of the whole animal, and not of details only ... as external shape and features provide not only an immediate means of recognition, but often also important systematic characteristics .... The literature on nudibranchs is full of detailed descriptions but too little of comparisons, which, however, are specially desirable in this group, because of the difficulty of finding representative characters in these soft-bodied animals ..."

During a comparative study of the nudibranch genus *Dendronotus* from the San Juan-Puget Sound area, Washington, I found that there were apparently 3 more species than were presently accepted names. In this paper I have redescribed the 6 known and accepted species {*D. frondosus* (Ascanius, 1774), *D. iris* Cooper, 1863, *D. robustus* Verrill, 1870, *D. gracilis* Baba, 1949, *D. albus* MacFarland, 1966, and *D. subramosus* MacFarland, 1966}. I have reinstated as well as redescribed two species, *D. dalli* Bergh, 1879 and *D. rufus* O'Donoghue, 1921, synonymized with *D. frondosus* by Odhner (1936). I consider *D. venustus* MacFarland, 1966 a synonym of *D. frondosus.* Finally, I have described a new species of *Dendronotus.*

For the sake of completeness, a diagnosis of the order, family, and genus, drawn from the literature, is included. I have included a definition or a figure or both of each taxonomically significant character referred to in this paper. Brief mention is made of a number of aspects of the nudibranchs' ecology and life history.

MATERIALS and METHODS

Because of the distinct ecological differences of the local species of *Dendronotus,* the animals were collected from a number of different areas from August 1966 to June 1967 (see Appendix I for longitude and latitude of the collection sites).

Dendronotus frondosus was collected from the moorage floats in Friday Harbor and Mitchell Bay during August, September, and early October of 1966 and again in April and May of 1967. During late October and throughout November, 1966, they were often found in the seawater tables at the Friday Harbor Laboratories. They have been

collected in February, 1967 and 1968, at Cantilever Pier in 35 m of water.

From June, 1965 to May, 1967, *Dendronotus iris* was collected incidentally while the research vessel, M. V. "*Hydah*," was otter trawling for flat fish in East Sound and Bellingham Bay. Occasionally, it was dredged in West Sound and Harney Channel. During June, 1967, I collected 15 animals while SCUBA diving at Departure Bay and Clarke Rock, Nanaimo, B. C.

Dendronotus subramosus was collected at Peavine Pass, Edwards Reef, Lonesome Cove, and Low Island during late August through to December, 1966 and in July, 1967. *Dendronotus rufus* was obtained from the outlet of the storm and sewer drain at Alki Point, Seattle during November through February of 1966 to 1967 and 1967 to 1968, respectively. *Dendronotus dalli* was collected on August 20, 1966; from October, 1966 to January, 1967, and from January 1 to 4, 1968, on the Victoria Breakwater, Victoria. *Dendonotus albus* was collected at Lonesome Cove, Brown Island, Collins Cove, and Edwards Reef from September to December, 1966. The new species of *Dendronotus* was obtained from Lonesome Cove, Brown Island, the Cantilever Pier, and the Victoria Breakwater from July, 1966 to January, 1967, although seldom in abundance. All of the species were collected less commonly in places other than those mentioned above.

The last 5 species I collected while SCUBA diving because survival is about 5 per cent when dredged and about 95% when collected while diving. Each animal plus its substratum, usually a hydroid, was placed in a plastic bag which could be tied shut and put in a canvas collecting bag. Ecological data, such as location, depths, currents, substratum, bottom type, possible food items, and reproductive activity were recorded on a sheet of 1.5 mm white matte plastic with a soft lead pencil.

Each nudibranch was kept in an individual container on the seawater table for about 2 days during which time the fecal pellets were examined to determine what the animal was eating prior to collection. A detailed description of each individual was then recorded on a prepared worksheet, special attention being paid to body proportions and dimensions, cerata, rhinophores, lip and veil papillae, color, and the ecological data mentioned above. A total of 15 *Dendronotus rufus*, 23 *D. subramosus*, 81 *D. albus*, 26 *Dendronotus* spec. nov., 28 *D. iris*, 32 *D. frondosus*, and 53 *D. dalli* were thus described. Many more specimens of each species were collected from May to September, 1967 and from January to March, 1968. They were checked to see if the above-mentioned characters fell within the range of variation described for the species.

To study the reproductive system, jaws and radula, each animal was relaxed with succinylcholine (Beeman, 1968), killed with 5% seawater formalin, and stored in 5% seawater formalin with 0.25% Ionol C. P.-40 (Robilliard, 1969).

The ducts of the isolated genital system were separated to facilitate study of the relative position and size of component parts. The "female gland mass," consisting of the fertilization chamber, "albumin" gland, membrane gland, and mucous gland (Ghiselin, 1965) was not drawn because the component parts are very fragile and cannot be easily separated. Furthermore, the size and shape of this organ depend very much on the reproductive activity of the genital system and are of minor taxonomic significance.

The excised buccal mass, placed in a petri dish, was left until all the tissue had decomposed. The radula was easily extracted from jaws, cleaned, and mounted in a non-resinous mounting medium (Turtox CMC-10). The jaws were washed and preserved in 5% seawater formalin. Both the radulae and the jaws were drawn using a camera lucida and the drawings were supplemented by reconstructions based on photographs.

Specimens of all the species studied have been deposited in the California Academy of Sciences, the Smithsonian Institution, and the Canadian National Museum.

SPECIES

Introduction to Species Descriptions

I have tried to use large samples of each species, consisting of animals from different localities, in order to account for the considerable intraspecific variation that occurs in the nudibranchs. Only living or well-relaxed, freshly preserved adult (or near-adult) animals have been described because of the paucity of very young specimens. The described animals are from a relatively limited area and there may be even more variation throughout their whole geographical range.

I have tried to compare and contrast each species with the other species by describing quantitatively (or qualitatively, if more appropriate) the same structure in each species. Where the description is quantitative, the first number(s) represents the mode of the measurements or counts, determined from all the animals used, followed by the range of variation enclosed in parentheses (e. g., body length, 5.0 - 6.0 (3.0 - 9.0) cm L).

Within the description of each species, I have tried to include the useful and accurate portions of earlier accounts. Because earlier authors generally have not em-

ployed a consistent nomenclature when referring to the anatomy and morphology of *Dendronotus,* I have applied distinct terms to each taxonomically significant structure and have defined and figured them. Although a few of the terms are original, most have been used before; synonyms and their references are included in Appendix II.

Except for the jaws, radula, and genital organs, the internal organs are not described as they appear to be very similar in all the species examined. For relatively complete descriptions and accurate diagrams of the internal organs, the reader is referred to Alder & Hancock (1845), Bergh (1894), Odhner (1936), and MacFarland (1966). The ganglia and nerves of the central nervous system, although slightly different in each species, are not described because they are difficult to isolate and the differences do not appear to be significant on the species level. Bergh (1879, 1894) and MacFarland (*op. cit.*) gave good descriptions and figures of the central nervous system.

The choice of important taxonomic characters is necessarily arbitrary (Mayr, 1965) but familiarity with a taxon prepares one, potentially at least, to choose those characteristics which will be most enlightening. After examining 7 species of *Dendronotus*, I have chosen several external and internal characters, listed below, on which I have based the species descriptions. These characters show the greatest intraspecific consistency while being demonstrably different interspecifically.

Six of the 9 named species of *Dendronotus* plus a new species were found in the study area. The other species, *D. robustus* and *D. gracilis,* are included for completeness, the description being based on a compilation of the available literature. This latter type of description is relatively unsatisfactory and should be used with some caution because of differences of opinion between biologists concerning the taxonomic significance of particular characters.

Synonymy and Taxonomic Remarks

Each synonymy cites only the first reference to a name or new combination of names that were already in use. To insure accuracy in the fairly exhaustive search for all the names used for a species of *Dendronotus*, I have tried to examine the original descriptions. When this has not been feasible, all other references concerning the elusive description were utilized. Where it is appropriate, I have made some remarks concerning the literary history of the species in an effort to indicate why certain authors felt new species should be established while others felt that lumping of certain species would be more realistic.

Body Form, Dimensions, and Texture

The body of *Dendronotus* is limaciform or "sluglike," but differences in body proportions determine whether or not the species is "delicate" or "heavy." The length (L) of the nudibranch is measured from the tip of the tail to the anterior edge of the veil between the two medial veil papillae when the animal is actively crawling (Figure 1).

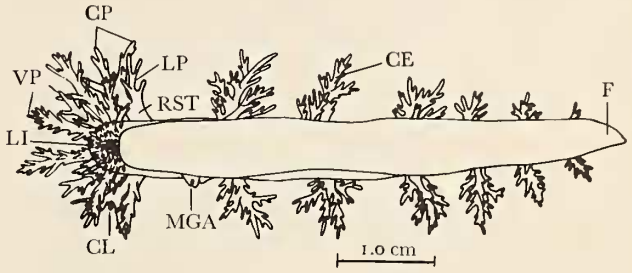

Figure 1

Ventral view of *Dendronotus dalli,* showing lip and veil papillae, position of the mouth, and the foot

CE = cerata CL = clavus CP = crown papillae
F = foot LI = lip papillae LP = lateral papilla
MGA = male genital aperture RST = rhinophore stalk
VP = veil papillae

The width (W) and height (H) are measured halfway between the first and second pair of cerata over the cardiac prominence, again when the animal is actively crawling (Figures 2, 3). The height is the distance from the substratum to the top of the cardiac prominence. The width is taken at the widest part of the body, exclusive of the edge of the foot, at the same point. These dimensions may vary more than 10% in a single animal because of its plasticity.

Texture refers to the surface of the epidermis. In most species, the epidermis is quite smooth, but in *Dendronotus frondosus, D. subramosus*, and a few *D. albus,* there are few to many conical (or subconical) papillae of various sizes scattered over the dorsum, particularly the cardiac prominence (Figure 3). They are usually capped with a yellow to cream colored pigment.

In all the specimens examined, the anus and genital orifice opened at approximately the same place. The anus, often on a raised papilla, is located about halfway along an imaginary line joining the bases of the 1st and

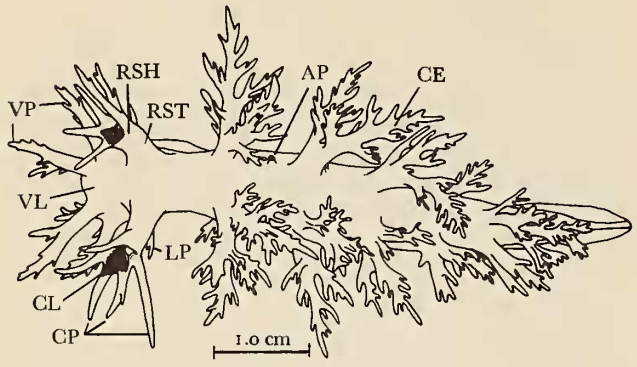

Figure 2

Dorsal view of *Dendronotus albus*, showing the external features of the body and appendages

AP = anal papilla CE = cerata CL = clavus
CP = crown papillae LP = lateral papilla
RSH = rhinophore sheath RST = rhinophore stalk
VL = veil VP = veil papillae

2nd cerata on the right side. The genital openings are located just anterior to the base of the 1st ceras on the right side, usually from $\frac{1}{3}$ to $\frac{3}{4}$ of the way up the side (Figure 3).

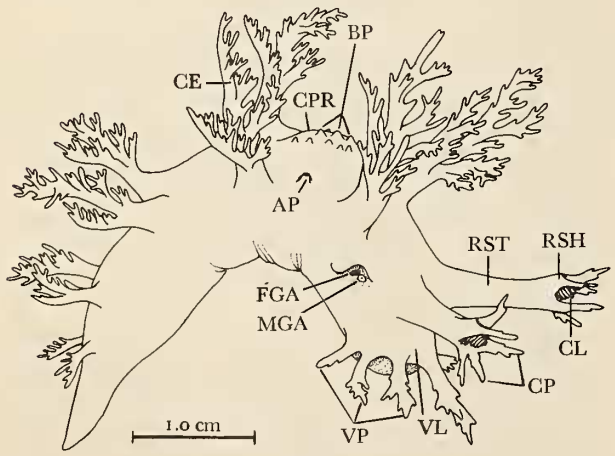

Figure 3

Lateral view of *Dendronotus subramosus*, showing the genital apertures and the cardiac prominence and papillae

AP = anal papilla BP = body papillae CE = cerata
CL = clavus CP = crown papillae
CPR = cardiac prominence FGA = female genital aperture
MGA = male genital aperture RSH = rhinophore sheath
RST = rhinophore stalk VL = veil VP = veil papillae

Foot

The foot (Figure 1) is briefly described, emphasis being placed on the length, width, shape, and functional aspects. The length (L) is the distance from the tip of the tail to the most anterior edge of the foot, while the width (W) is measured as the widest part of the foot. Both measurements are taken while the animal is crawling. The discussion of the functional aspects of the foot, particularly in relation to the animal's feeding habits, is based partly on field and laboratory observations and partly on speculation. Further studies are being made to determine the relationship between the morphology of the foot and the animal's feeding habits.

Color

Color is one of the most variable characters in *Dendronotus*. However, if the variations are recognized and some caution is exercised, color can be used as a guide in identifying the species. In many cases, there are distinct patterns (cf. *D. subramosus*) that occur consistently and allow one to identify the animal even though the ground color is different. As a final guide, color plates are presented (Plates 63 and 64).

Cerata

The term cerata (Figures 2, 3) should probably be reserved for the dorsal appendages of the Aeolidiacea (Morton, 1958), but, because the term has been more or less accepted, and because it distinguishes between dorsal processes (rhinophores and "cerata"), I have used it in this paper. The possible function of the cerata as respiratory organs is evident from the nomenclature that has been applied by previous authors (see Appendix II) although there has been no experimental work done to prove this. Some aeolids have cerata with cnidosacs which presumably are for protection (Edmunds, 1966), but there appear to be no cnidosacs in *Dendronotus* (Pruvot-Fol, 1954; Thompson, 1960a). Other aeolids are able to autotomize the cerata as a possible protective mechanism (Edmunds, *op. cit.*; Garstang, 1889; Stasek, 1967; Thompson, 1964), but the dendronotids appear unable to accomplish this feat (unpublished observations). I have, however, examined a number of specimens which have lost parts of or whole cerata, rhinophores, or veil papillae, probably from attacks by predators such as fish.

The branching patterns (Figure 4) and the size of the cerata are relatively distinct and consistent within a species. Each ceras has 1 - 5 main branches, defined as those large branches arising directly from the body or from very

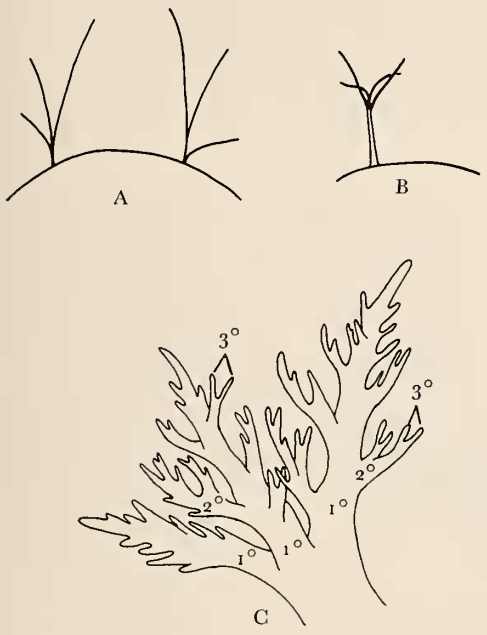

Figure 4

Branching patterns of cerata
A. "Fan-shaped" pattern with the left ceras showing all 3 branches arising from a single stalk while the right ceras shows the lateral branch arising first and the medial 2 arising above this.
B. "Rosette" pattern.
C. Primary (1°), secondary (2°), and tertiary (3°) branching of a single ceras.

near the base of the ceras. From these main branches arise a few to many secondary and tertiary branches (Figure 4c). Normally the medial main branch is the longest, the others becoming progressively shorter with the lateral branch being the shortest. In some species, *e. g.*, *Dendronotus iris,* it is difficult to distinguish the main branches from large secondary branches and the choice becomes arbitrary. There are two basic patterns which I have called the "fan-shaped" pattern (Figure 4a) and the "rosette" pattern (Figure 4b). The "fan-shaped" ceras is oriented with the "fan" at right angles to the long axis of the body. The "rosette" pattern consists of the branches radiating from the top of a stout stalk. In a few specimens, particularly of *D. rufus,* there are small tufts called "accessory" cerata appearing in irregular groups between the main cerata, especially over the cardiac prominence.

The first pair of cerata usually is the largest with successive posterior pairs becoming smaller and less branched. The distance between successive pairs usually decreases posteriorly. The reduction in the number of main branches appears to be due to the loss of the lateral branches.

Rhinophore and Clavus

It has been generally thought that the rhinophores, particularly the clavus, "on the basis of their position, structure and innervation" (Kohn, 1961, p. 300) are used as chemoreceptors, especially for the detection of food. Most of the experimental work with food extracts has failed to show conclusively that the rhinophore is any more sensitive to chemosensory stimulation than any other part of the cephalic region (Kohn, 1961). However, Wolter (1967) has shown that the rhinophore is a chemosensory structure, stimulated by food, in *Archidoris tuberculata, Polycera quadrilineata, Aeolidia papillosa,* and *Facelina drummondi.*

The 3 important components of the rhinophore are the lateral papilla, the crown papillae, and the clavus (Figures 2, 3) (see Appendix II for synonyms). The presence or absence, size, pattern of branching, and point of origin on the rhinophore stalk are important in describing the lateral papilla, the function of which is unknown. The crown papillae, vertical prolongations of the rhinophore sheath, vary in length, number, degree of branching and arrangement on the sheath. The leaves of the clavus vary in size, shape, number, and color. The overall shape of the clavus is also important. In some cases, the position at which the rhinophores are held while the animal is crawling is distinctive.

Head, Lips, and Veil

The cephalic region of *Dendronotus* is very sensitive and there is a strong indication that the veil papillae, and possibly the lip papillae, serve as contact chemoreceptors (unpublished observation) as do the oral tentacles of some aeolids (Kohn, 1961). As well as indicating the existence of food, the veil papillae may warn the nudibranch of a potential predator. When the animal crawls, the veil papillae are held upward and forward. As soon as they contact anything unfamiliar or different from the immediate surroundings, the animal retracts and then cautiously extends itself, exploring the area with the veil papillae. If it is unpleasant, the nudibranch will turn away. If, however, it is food, *Dendronotus* advances immediately and begins to feed. In all the local species which feed on hydroids, there are some indications that the lip papillae

are used to orient the mouth and lips parallel to the long axis of the hydroid stalk. The jaws may then be effectively employed in holding the stalk while the radula rasps through the perisarc, and the animal can withdraw the coenosarc easily.

The most important taxonomic features of the head region (Figures 1 to 3) are the number, degree of branching, and arrangement of the veil and lip papillae. The color of the lips is also distinctive in some cases. No attempt was made to describe the inner labial ring and other mouth armature described by MacFarland (1966).

The veil papillae have been arbitrarily defined as those papillae which originate in a single row from the most distal edge of the more or less distinct, horseshoe-shaped veil. The lip papillae are all those papillae in the ventral cephalic region not included in the above. In some species, such as *Dendronotus rufus,* the lip papillae may be as long as the shorter veil papillae and more branched, but their position establishes their relationship. The lip papillae may be arranged in vaguely regular rows. It must be emphasized that this definition of the papillae may be artificial as it is based on position, not function.

To facilitate identification of any particular pair of veil papillae they are numbered from medial to lateral, the medial pair being pair no. 1 (Figures 2, 3).

Jaws

The jaws of *Dendronotus,* enclosing most of the buccal mass, provide attachment for the jaw and radula muscles. The functional portion of the jaw is the masticatory process which is responsible for holding the prey and possibly chops off pieces of the prey as it is pulled into the mouth by the radula. Inferences about the species' feeding habits may be made from the structure of the jaw and its size relative to the size of the animal.

The descriptions and diagrams (Figures 5, 7, 10, 13, 16, 19, 22, 25) attempt to point out differences in shape and relative proportions of the jaw components. With the exception of *Dendronotus iris,* the jaws are fairly uniform morphologically within the genus and one must exercise caution in attempting to identify the species of *Dendronotus* from the jaws alone.

For a fairly complete description and excellent drawings of the jaws of some species of *Dendronotus,* the reader is referred to MacFarland (1966). He includes a detailed description of the denticulation on the masticatory border of the jaw, but I feel that this is not a particularly useful taxonomic character, partly because of the difficulty in examining the denticles, and partly because of the considerable intraspecific variation and interspecific overlap in number and shape.

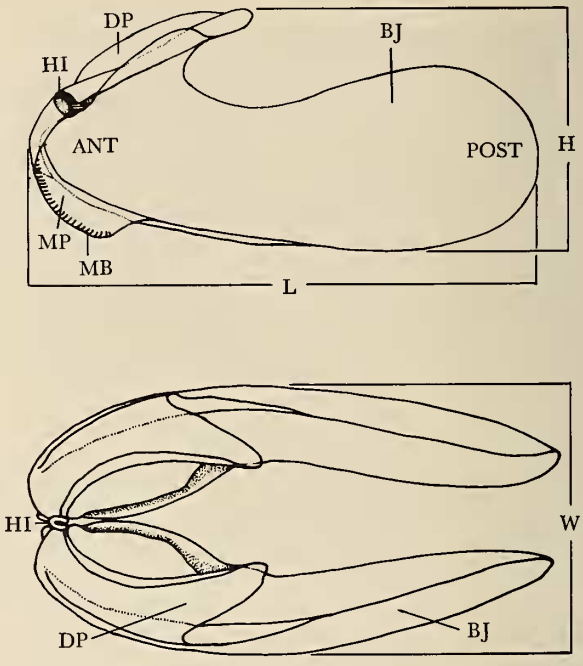

Figure 5

Measurements and components of a *Dendronotus* jaw
A. Inside lateral view B. Dorsal view
ANT = anterior BJ = body of jaw DP = dorsal process of jaw
H = height HI = hinge of jaw L = length
MB = masticatory border MP = masticatory process
POST = posterior W = width

Radula

The radula of nudibranchs (Figures 8, 11, 14, 17, 20, 23, 26), as in most other mollusks, serves as a rasping organ which, operated by a complicated series of muscles, moves back and forth over the odontophore pulling food into the pharynx. However, descriptions of the radular musculature and other functional considerations of the buccal mass are left for future work.

Because the basic shape of the median and lateral teeth is essentially the same in all the species, the reader is referred to MacFarland (1966) for a relatively detailed descripion of these teeth in 4 species. The width-height ratio for the median tooth (see Figure 6 for measurements) referred to in this paper is not the same as that of Garstang (1890), MacFarland (1966) or O'Donoghue (1921); it was used because of the ease with which it could be measured. This ratio usually decreases, some-

times markedly, from the anterior, well-worn teeth to the posterior, unused teeth.

The denticulation and number of the median and lateral teeth of the radula are taxonomically important. For purposes of this paper, the lateral teeth in a transverse row are numbered from medial to lateral, number 1 being

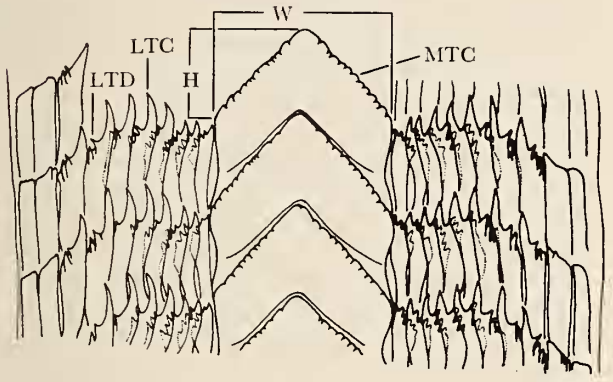

Figure 6

Measurements and components of a generalized *Dendronotus* radula
H = height LTC = lateral tooth cusp
LTD = lateral tooth denticle MTD = median tooth denticle
W = width

adjacent to the median tooth. The rows are numbered from oldest to newest, number 1 row being the oldest.

The denticulation is a striking feature of the radula of *Dendronotus*. Along the cutting edge of the triangular cusp of the median tooth, there may be: a few relatively large, sharp denticles; many small denticles giving a serrulated appearance; no denticles at all; or any combination of these three. These denticles may be limited to the proximal half of the cusp or they may extend along its whole length, in which case the denticles generally decrease in size towards the apex of the cusp. The denticles of the lateral teeth are limited to the outer margin of the sharp, curved cusp although they and the cusp are usually absent from the innermost teeth. These denticles vary in size, number, and shape, but there is an intraspecific consistency and interspecific dissimilarity which aids in classifying these nudibranchs.

Reproductive System

Dendronotus has a triaulic genital system (Figures 9, 12. 15, 18, 21, 24, 27, 28) with the penis completely separate and the "female portion split longitudinally in an uterine and a vaginal portion which communicate proximally and distally" (Odhner, 1936, p. 1071; see also Eliot, 1910; Ghiselin, 1965). No attempt was made to determine the exact relationships and functions of the various structures in this triaulic system, but the following scheme, based on reports on related genera and families (Ghiselin, *op. cit.*; Odhner, *op. cit.*; Thompson, 1961) is probably reasonably accurate.

The hermaphrodite gland or ovotestis, composed of numerous tightly packed round to pyriform lobules, produces both ova and sperm. The central rounded follicle contains developing spermatogonia and mature sperm, while the developing ova surround these male follicles (MacFarland, 1966). A thin tube arises from this lobule to join others, eventually forming the hermaprodite duct through which gametes course to the ampulla where the sperm are stored prior to copulation (Ghiselin, 1965, p. 331). There is some evidence that the sperm are produced first and, after copulation, are stored in the seminal receptacle of the partner until the ova ripen (Ghiselin, *op. cit.*, p. 343; but see also Thompson, 1961, p. 10). There is a short spermoviduct joining the ampulla to the bifurcation that leads to the vas deferens and the oviduct. Possibly there is a valve at this bifurcation that functions much the same way as it does in *Tritonia hombergi* to separate endogenous gametes and send them along the proper ducts (Thompson, *op. cit.*).

The sperm travel along a short duct, the proximal portion of the vas deferens, leading to the prostate portion of the vas deferens. The function of the prostate, composed of varying numbers of large or small glandular alveoli, or both, is poorly known (Ghiselin, *op. cit.*, p. 331). Odhner's suggestion (1936, p. 1070) that the external appearance of the prostate may be species specific has been verified in this study. The distal portion of the vas deferens, which probably secretes some of the prostatic secretions, continues from the prostate to the penis. This distal portion may be short and thick (*Dendronotus dalli,* Figure 15) or it may be long and tortuous (*D. rufus,* Figure 18). It continues to the penis tip as the convoluted, tapered ejaculatory duct. The unarmed penis, enclosed within a preputium opening to the outside, varies considerably in size and shape.

The female system begins at the bifurcation of the spermoviduct as the oviduct. This leads to the fertilization chamber and subsequent parts; "albumin gland," membrane gland, and mucous gland (Ghiselin, *op. cit.*, p. 334). Just before the oviduct enters the fertilization chamber, an insemination duct, which subsequently dilates to form the seminal receptacle, arises. From the seminal receptacle, the vagina courses to the common female cavity or vestibule into which the "female gland mass" also opens. Near the opening of the vagina, there is a small bursa copulatrix which may

not be functional (GHISELIN, *op. cit.*, p. 334; ODHNER, *op. cit.*, p. 1107).

Copulation in *Dendronotus* seems to be reciprocal, the penis of each partner being inserted into the vagina of the other. At present, the exact place where the sperm is deposited is an enigma, but the length of that portion of the penis that is inserted into the partner suggests that it is in the seminal receptacle. The exogenous sperm is probably stored in the seminal receptacle (as indicated above) where it may be rendered physiologically active by secretions from the epithelium (THOMPSON, *op. cit.*). From here, it travels to the fertilization chamber, via the insemination duct, to fertilize the endogenous ova. The zygote follows a predetermined path through the "female gland mass" where the primary egg capsules, nidamental layers, and other necessary mucus coats are added prior to oviposition (GHISELIN, 1965; THOMPSON, 1961). The egg masses are Type B (HURST, 1967).

Geographical Distribution

At present, the distribution records for the species of *Dendronotus* suggest that the genus is restricted to the north temperate and arctic seas. With the exception of one record of *D. albus* from Islas Los Coronados, Mexico (Lance, pers. comm.), none have been described from the sub-tropical or tropical seas. So far, the only record from the seas of the southern hemisphere is 2 small specimens of *D. gracilis* (Miller, pers. comm.). This type of distribution is possibly directly related to the collection effort, but it may represent an actual biological phenomenon caused by so far unknown causes. Further investigations would be desirable to clarify this situation.

As far as possible, all geographical areas where a species of *Dendronotus* has been found are recorded. The records for *D. frondosus* are extensive and have been condensed.

Ecology

No species description should be considered complete unless some indication of the species' life history and ecology is given. Yet, very little has been published concerning the ecology of *Dendronotus*. The food preference of *D. frondosus* has been briefly mentioned by a few authors (MILLER, 1961; SWENNEN, 1961; THOMPSON, 1964; WATERS, 1966). HURST (1967), MACFARLAND (1966), MILLER (1962), SWENNEN (1961), and others report briefly on various aspects of the reproductive biology of *D. frondosus*. There are numerous rather extensive reports on the geographical distribution of *Dendronotus* (BERGH, 1894; MARCUS, 1961; ODHNER, 1926) giving collection sites and occasionally depth. However, no description is given of the hydrography or of the substratum, and both are important in understanding the ecology of the nudibranch.

More complete ecological studies will be the subject of another paper, but the data presented here indicate trends and are useful both for taxonomic purposes and as a guide for further ecological studies. The physical data collected include depth, current action, and composition of the bottom (rock, mud, shell-gravel, etc.). The immediate substratum (hydroid, rock, etc.) of the animal at the time of collection plus the presence (or absence) and abundance of potential food items is noted.

Some aspects of the reproductive biology such as copulation in the field and laboratory, and degree of gonadal development are recorded. In some cases, a description of the egg string, its location in the field, and length of time from oviposition to hatching of the veliger is presented.

Brief descriptions are made of the feeding processes where seen or where reported. A more detailed report of these processes will be the subject of a future publication.

Comments concerning the possibility of cryptic or warning coloration as well as some methods of defense against, or escape from, predators are made where appropriate.

Dendronotacea

This name was first used by ODHNER (1934) to include a number of families and genera (ODHNER, 1936). This suborder is characterized partly by the structure of the liver but, more importantly, by the fact that the clavus of the rhinophore is retractable into the rhinophore sheath (ELIOT, 1910; ODHNER, 1934, 1936) and by the branched cerata on the notum. The latter are found in all the species of the Dendronotacea to a greater or lesser degree.

DENDRONOTIDAE

Dendronotus ALDER & HANCOCK, 1845

At present, the family has only one genus, *Dendronotus*. On the basis of a reduced branching of the cerata, crown papillae, and veil papillae compared to *Dendronotus* (ELIOT, 1910), BERGH (1863) established the genus *Campaspe* to include the species *C. pusilla* and later, *C. major* BERGH, 1886. ELIOT (1910) and ODHNER (1936) conclude that BERGH was actually describing juvenile specimens of *D. frondosus*. ODHNER (*op. cit.*, p. 1105) states that:

> "Since the genus *Campaspe* BERGH 1863, to which BERGH referred two species established by himself, cannot be separated from *Dendronotus* and is based on juvenile specimens of *D. frondosus* ..., the family includes [a] single member the genus *Dendronotus*."

Those features characterizing the genus also necessarily apply to the monotypic family. The following compendium of characters has been compiled from the family or genus diagnoses of Eliot (1910), Odhner (1936), Pruvot-Fol (1954), Thiele (1929-35).

Body limaciform; 4 - 8 pairs of arborescent cerata, one of each pair on either side of the dorsum; cerata lacking cnidosacs and any special gill (present in the Dotonidae); relatively distinct veil supporting 2 - 5 pairs of more or less branched veil papillae; clavus of rhinophore perfoliate with 8 - 30 leaves; top of rhinophore sheath extended as 4 - 6 more or less branched crown papillae; a lateral papilla originating from the lateral border of the rhinophore stalk; anal papilla between first and second cerata on the right side; genital openings anterior and ventral to base of the first ceras on the right side; liver in 3 parts, one large posterior portion and 2 smaller anterior portions; hepatic diverticula may extend into some or all of the cerata and rhinophores; no stomachal plates; salivary gland long; relatively strong jaws; radula narrow to moderately wide (6-1-6 to 21-1-21); median teeth with smooth or denticulated cusp; lateral teeth narrow, pointed, usually denticulated; triaulic genital system; prostate present; bursa copulatrix small; penis unarmed.

Dendronotus frondosus (Ascanius, 1774)

(Plate 63, Figure 29; Text figures 4, 7, 8, 9)

Amphitrite frondosa Ascanius, 1774, K. Norske Vidensk. Selsskabs Skrifter, Deel 5: 155; plt. 5, fig. 2

Doris arborescens Müller, 1776, Zoologiae Danicae Prodromus, p. 229

Doris cervina Gmelin, 1791, Syst. Nat. per Regna Tria Nat., 13th ed., 1 (6): 3105, no. 12

Tritonia arborescens Cuvier, 1817, Ann. Mus. 6: 434; plt. 6, figs. 8 - 10

Tritonia reynoldsii Couthouy, 1838, Boston Journ. Nat. Hist. 2 (1): 74; plt. 2, figs. 1 - 4

Tritonia lactea Thompson, 1840, Ann. Nat. Hist. 5: 88; plt. 2, fig. 3

Tritonia pulchella Alder & Hancock, 1842, Ann. Mag. Nat. Hist. 9: 33

Dendronotus arborescens (Müller, 1776). Alder & Hancock, 1845, Ray Soc. Monogr., Fam. 3, plt. 3, prt. 1

Amphitritidea fabricii "Beck 1847." Mörch, Grönland (Rink) (Prodr. Fauna Moll. Gronl., p. 6), 1857; in synonymy [this reference has been taken directly from Iredale & O'Donoghue, 1923]

Dendronotus luteolus LaFont, 1871, Act. Soc. Linn. Bordeaux, 28: 287; plt. 17, fig. 1

Dendronotus purpureus Bergh, 1879, Proc. Acad. Nat. Sci. Philadelphia, art. 5: 145 - 150; plt. 1, figs. 18 - 20; plt. 3, figs. 7 - 12

Dendronotus purpureus var. *aurantiaca* Friele, 1879, Jahrb. Deutsch. Malakozool. Gesellsch. 6: (page unknown) [reference unavailable]

Campaspe pusilla Bergh, 1863, Naturh. Tidsskr., 3 R., 1: 471 - 478; plt. 12, figs. 28 - 35

Campaspe major Bergh, 1886, Bidjr. Dierk. 13: 21 - 24; plt. 1, figs. 23 - 26; plt. 2, figs. 1 - 11

Dendronotus frondosus (Ascanius, 1774). Plymouth Marine Invert. Fauna 1904. Journ. Marine Biol. Assoc. U. K. 7: 282

Dendronotus lacteus (Thompson, 1840). Eliot, 1910, Ray Soc. Monogr. Suppl., Fam. 2, genus 1, p. 161

Dendronotus venustus MacFarland, 1966, Mem. Calif. Acad. Sci. 6: 271 - 275; plt. 40, fig. 2; plt. 46, figs. 9 - 12; plt. 47, figs. 1 - 2; plt. 49, fig. 6; plt. 50, fig. 3; plt. 52, figs. 3 - 6

Taxonomic Remarks

The above references are only part of a fairly extensive, and often conflicting, literature concerned mainly with taxonomy, morphology, and geographical distribution of *Dendronotus frondosus*.

The description by Ascanius (1774) is sufficient to establish that *Amphitrite frondosa* is the same animal as *Doris arborescens* Müller, 1776. Thus the name *Amphitrite frondosa* takes priority. However, the generic name is unavailable because it is used by O. F. Müller in 1771 for a genus of polychaetes. Because *A. frondosa* is not the type species for either the genus *Doris* or *Tritonia*, nor is it a member of either of these genera, the species must be placed in the next available genus, *Dendronotus*, established by Alder & Hancock (1845). They distinguished *Dendronotus* from *Tritonia* on the basis of rhinophore structure, the lack of a sub-pallial ridge on the dorsum, free arborescent cerata, and the structure of the liver. However, they used the species name *arborescens* apparently unaware of the existence of *frondosa*. The first time *Dendronotus frondosus* was used appears to be in the Plymouth Marine Invertebrate Fauna (1904). Probably Eliot was responsible for this change (see Eliot, 1910) although no reference is made to him. Subsequent authors have used both *D. frondosus* and *D. arborescens*, but the correct name is *Dendronotus frondosus* (Ascanius, 1774).

Biologists of the 18th and 19th centuries added to the confusion by describing a number of "new species" (*Dendronotus luteolus, D. purpureus, D. lacteus*) as well as a "new genus," *Campaspe*. All of these are almost surely synonyms of *D. frondosus*.

Odhner (1936) used *Dendronotus frondosus* as a catch-all for all the previously described species except *D. robustus* and *D. iris*. He maintained that *D. frondosus* was a highly polymorphic species and that the other described species were well within the limits of variability

to be expected from this polymorphic species (see under *D. dalli* and *D. rufus* for further discussion).

Dendronotus venustus represents a case of splitting. Except for color, this species is very similar to *D. frondosus*. I have collected a few specimens which, in color, intergrade between these two nominal species, particularly with reference to the white patches found between the cerata by MacFarland. In his field notes (deposited at the California Academy of Sciences), MacFarland describes color phases of *D. venustus* which are identical with *D. frondosus*. Lance (pers. comm.) is also of the opinion that *D. venustus* is a synonym of *D. frondosus*.

The descriptions of *Dendronotus frondosus* by Marcus (1961) and MacFarland (1966) confuse 3 or 4, and 3, distinct species, respectively.

Body Dimensions, Texture, and Apertures

The limaciform, laterally compressed body is moderately "heavy." The rounded dorsum tapers posteriorly to a long, sharply pointed tail and merges laterally with the vertical sides.

The largest animal collected was 4.2 cm L while the largest reported are 5.5 - 6.0 cm (Bergh, 1879, 1894), 9.8 cm L (Swennen, 1961), and 11.5 cm L (MacGinitie, 1959). The smallest animal I collected was 0.2 cm L. Most, however, have been 1.0 - 3.0 cm L with only a few being longer than 3.5 cm.

The anus is borne on a distinct papilla, often capped with a yellow pigment, and located halfway between the first and second right cerata.

The genital apertures open externally about $\frac{2}{3}$ of the way up the right side of the body, just anterior to the base of the first ceras.

The cardiac prominence is large and often rises 4 - 5 mm higher than the dorsum. The body is covered with bluntly conical papillae of various sizes that are usually tallest on the cardiac prominence. A distinctive characteristic of this species is the yellow or white pigment that caps these papillae; only rarely is it missing.

Foot

The long, relatively narrow foot is bluntly rounded anteriorly and tapers to a short, pointed tail. The sole is white and translucent.

The edge of the foot flares along its entire length when the animal is crawling on a smooth surface. It is able to adhere more firmly than other species to smooth surfaces. When on a hydroid, the edges of the foot wrap around the stalk allowing the nudibranch to adhere firmly to the hydroid.

Color

The translucent, gray-white ground color of the animal is overlaid with varying concentrations of brown, red-brown, yellow, and white pigments in assorted patterns (Plate 63, Figure 29). To the naked eye, some of the animals have a reddish-brown hue, streaked and marbled with brown and spotted with yellow and white while others are very pale tan with numerous yellow spots. A few, particularly those from deeper water (more than 25 m), lack all pigment and appear white.

In about 50% of the animals, the body was brown with a sparse scattering of white and yellow spots, but the distal portions of all the body processes were devoid of brown and appeared transparent or yellowish. A few animals were devoid of light pigments, while a few others were devoid of any brown but were liberally covered with yellow or white or both (see Alder & Hancock for coloration and pattern).

The pinkish-brown hepatic diverticula and liver are clearly visible through the body wall as is the white hermaphrodite gland.

Cerata

The 5 - 7 (4 - 8) pairs of tall, erect cerata are arranged at posteriorly decreasing intervals. The height and degree of branching also decreases posteriorly. In a few specimens, there are 1 - 4 small, unbranched, unpaired cerata on the posterior end.

The cerata are more arborescent than in the new species of *Dendronotus,* but less so than in *D. rufus* or *D. iris*. The main branches, quite tall and slender, give rise to numerous relatively long secondary and tertiary branches that end in pointed transparent tips.

The pattern of main branches is typically "fan-shaped" (Figure 4a) with 3 main branches in the first 3 pairs, 2 - 3 in the 4th pair, 1 - 2 in the 5th, and one in the rest. In those pairs with 3 main branches, the medial is the tallest while no. 2 branch is about $\frac{3}{4}$ as long and arises just above the lateral. The lateral branch, arising right at the base of the ceras, is about $\frac{1}{3}$ to $\frac{2}{3}$ as long as the medial and diminishes in size from the anterior to the posterior cerata.

The hepatic diverticula appear to be present in the anterior 4 - 5 pairs of cerata, usually in the medial 1 - 2 main branches as well as the rhinophores. These diverticula in the first pair of cerata and the rhinophores originate from the anterior lobes of the liver and the rest arise from the posterior lobe.

Rhinophore and Clavus

The moderately branched rhinophore is about equal in height to the first pair of cerata.

The lateral papilla, arising between a quarter and halfway up the stalk, is relatively long, often extending as high as or higher than the clavus. The degree of branching is variable; some are simple papillae, most have a few short, simple secondary branches, and a few are very branched, much like the cerata.

The sub-conical perfoliate clavus bears 8 - 12 shallow-cut leaves that alternate in width. There are a few reports of up to 20 - 25 leaves in larger animals (Bergh, 1894, 1900) and I have seen as few as 5 - 6 in smaller ones. The coloration of the clavus is similar to that of the rest of the body.

There are usually 5 (4 - 6) long, stout crown papillae having little or no secondary branching. The postero-medial papilla may be 1 - 3× as long as the 3 anterior papillae which are usually about equal in length. The postero-lateral may be about twice as long as the anterior ones.

Head, Lips, and Veil

In size, number, and branching, the veil papillae seem to come midway between the condition found in *Dendronotus rufus* and *D. dalli,* and that of *D. albus.*

There are 4 pairs of relatively stout, branched veil papillae. On the larger pairs, the branching may be extensive, much like the cerata, or it may be confined to a few small papillae. The smaller pairs are often unbranched, sometimes have a few small papillae, or, rarely, they may be extensively branched. The medial pair (no. 1) is the longest, no. 2 is the shortest at about ¼ to ½ as long, no. 3 is slightly shorter than no. 1, and no. 4 is about ⅔ as long as no. 1.

There are 2 - 4 (0 - 8) long, thin, simple lip papillae located lateral and posterior to the plicated lips. These papillae are sensitive to touch and retract almost completely when stimulated mechanically.

Jaws

The body of the jaw (Figure 7) is a translucent dingy-yellow which becomes dark brown, almost black on the masticatory process, hinge, and proximal portion of the dorsal process. The body is a shallowly convex, almost oblong structure about 2½× as long as wide with a moderately convex posterior end.

The slightly curved, rather wide dorsal process is inclined posteriorly at 55° - 60° from the long axis of the body. It is about 0.41× as long as the body of the jaw and has a shallow dorsal groove. A thin, strongly convex lateral expansion joins the proximal ⅔ of the process to the body. The moderately long, curved masticatory process, often sharply hooked at the free end, is joined by an almost flat, strong expansion to the body. A small number of relatively large, black denticles adorns the masticatory margin.

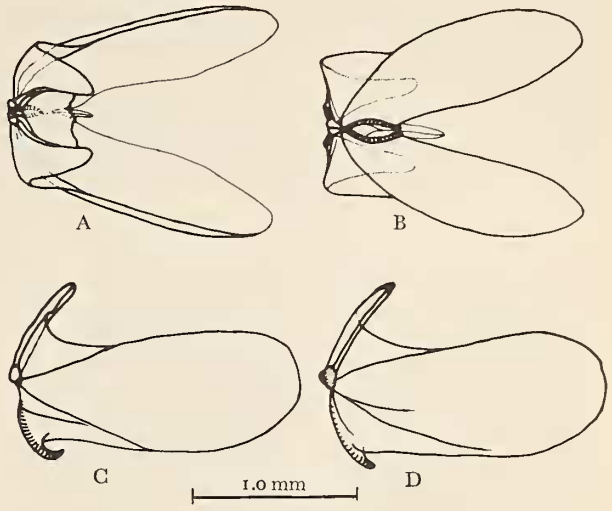

Figure 7

Dendronotus frondosus jaw
A. Dorsal view B. Ventral view C. Outside lateral view
D. Inside lateral view

Radula

The radula (Figure 8), described a number of times (Alder & Hancock, 1845; Bergh, 1879, 1894, 1900; Meyer & Möbius, 1865; O'Donoghue, 1921), varies widely in the number of rows of teeth present, but this appears to be directly correlated with the length of the animal. The radula formula, from the literature, is 29 - 49(7 - 14 · 1 · 7 - 14) and from those I examined (10 specimens), it is 33 - 48(7 - 11 · 1 ·7 - 11). Bergh (1894) and Volodchenko (1955) report that they found golden-yellow teeth in their specimens, but all those I examined were colorless.

The cusp of the median tooth, about 1.4 - 1.7× as wide as high, comes to a relatively sharp point. There are 7 to 15 large, strong, sharp denticles on the sides of the cusp, usually becoming smaller towards the apex. In the anterior teeth, there are fewer denticles and they tend to

disappear near the apex while the posterior teeth have more denticles extending along the whole side. The lateral edge of the denticles continues down the dorsal side of the cusp as a deep furrow.

The elongate, relatively wide lateral teeth bear long, curved cusps inclined 10° to 20° toward the midline. They are usually rather longer than shown in Figure 8.

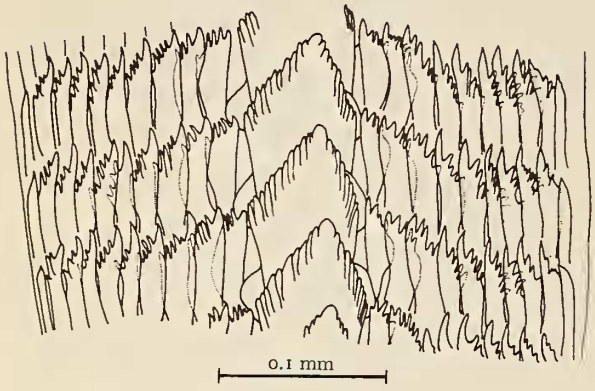

Figure 8

Dendronotus frondosus radula
Rows 25 to 27 in a radula with 45 rows of teeth

On the innermost 1 - 3 teeth, the cusp is often no longer than the denticles while in the outermost 1 - 2, the cusp may be missing or rudimentary. The size is about equal in the rest. From anterior to posterior, within a single radula, the cusps tend to become longer and fewer are broken off.

All the teeth, except the outer 1 - 2, bear 2 - 5 (0 - 7) long, strong, sharp, regularly spaced denticles on the lateral margin of the cusp.

Reproductive System

The large, white hermaphrodite gland gives rise to a long hermaphrodite duct that widens suddenly into a wide ampulla curled up like a doughnut (Figure 9). The long, narrow spermoviduct arises from the other end of the ampulla but runs alongside the hermaphrodite duct for a short distance. The proximal portion of the vas deferens and the oviduct are both short, translucent and quite narrow.

Odhner (1936) reports and figures the prostate as being "... a circular disc composed of numerous scattered vesiculae [= alveoli] (fig. 39a), in many circles ..."

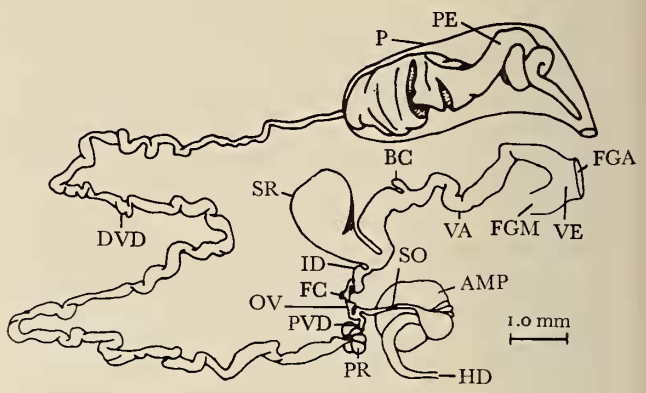

Figure 9

Reproductive system of *Dendronotus frondosus* (exploded view)
AMP = ampulla BC = bursa copulatrix
DVD = distal vas deferens FC = fertilization chamber
FGA = female genital aperture FGM = (to) female gland mass
HD = hermaphrodite duct ID = insemination duct
OV = oviduct P = preputium PE = penis PR = prostate
PVD = proximal vas deferens SO = spermoviduct
SR = seminal receptacle VA = vagina VE = vestibule

However, I rarely saw more than 12 and usually only 5 - 8 large, ovoid alveoli arranged as a disc concentric with the vas deferens. From the prostate arises a very narrow, long, convoluted, almost untapered distal portion of the vas deferens. It enters the penis to become a much convoluted ejaculatory duct. The very long, thin penis, tapered to a point and coiled up in the preputium, has a pleated base.

The long, convoluted vagina empties into the large, sessile, pear-shaped seminal receptacle. The distal end of the vagina opens into the vestibule quite near the external orifice. A small, stalked bursa copulatrix is located about $\frac{3}{4}$ of the length of the vagina away from the vestibule. The insemination duct is moderately long and convoluted.

The reproductive system described and figured by MacFarland (1966) for *Dendronotus venustus* agrees closely with that of *D. frondosus,* further evidence that *D. venustus* should be considered a synonym of *D. frondosus.*

Geographical Distribution

Dendronotus frondosus, a north circumpolar species, has been reported from Arctic seas and the northern Atlantic and Pacific Oceans. More exact locations include the coast of Norway (Odhner, 1926, 1939), Point Barrow,

the Bering Sea, the east coast of North America from Labrador to Cape Cod, Greenland, the Faroes, the Shetlands, Spitzbergen, and the western Arctic (MacGinitie, 1959), the eastern Atlantic south to the Bay of Biscay (Bergh, 1894), and the Baltic Sea as far as Kiel Bay (Swennen, 1961). It has also been found on the northern Asiatic coast (Baba, 1957; Volodchenko, 1955) and along the Eastern Pacific Coast from Alaska to Southern California (Lance, pers. comm.; unpublished observation). Kerry Clark (pers. comm.) has collected a number of specimens from the coast of Connecticut.

Ecology

Despite the number of descriptions of the species, there has been surprisingly little published about its biology. Brief mention has been made of its food and substratum preferences, and the reproductive cycle (Miller, 1961, 1962; Swennen, 1961; Thompson, 1964; Waters, 1966).

Locally, the species has been collected from April to the beginning of December from floating wharves in Friday Harbor and from June to March in the sub-tidal down to 40 m. Swennen (1961) reports finding *Dendronotus frondosus* all year long at Den Helder. Other reports (Miller, 1962) would indicate *D. frondosus* are probably present as adults, in greater or lesser numbers, throughout the year. Mr. K. Clark (pers. comm.) has found specimens in May, but not in summer, in Connecticut.

Dendronotus frondosus ranges from the inter-tidal to 400 m+ (Swennen, 1961) and is present on rocky as well as muddy bottoms and styrofoam floats, where numerous hydroid colonies are present.

Dendronotus frondosus appears to be a feeding specialist on hydroids, but is flexible about what species it will eat. It has been reported to feed on *Tubularia indivisa* and *Sertularia cupressina* (Swennen, 1961), *Syncoryne eximia, Bougainvillia glorietta,* and *Obelia commissuralis* (Waters, 1966), *Tubularia larynx* (Braams & Geelen, 1953), *Dynamena pumila, Hydrallmania falcata* and *Sertularia argentea* (Miller, 1961), and *Tubularia crocea* (K. Clark, pers. comm.). There is also some evidence that the younger animals prefer one species of hydroid while the adults prefer another (Swennen, *op. cit.*). Noting this, Miller (1961, p. 105) says:

> "... small specimens (1 - 18 mm) of *Dendronotus frondosus* feed on both gymnoblastic and calyptoblastic hydroids, large specimens (14 - 100 mm) only on gymnoblasts (*Tubularia* spp.). The large polyps of *Tubularia* probably provide a fairly large volume of food in a form which can be grazed easily and rapidly, supplying a quantity sufficient for the needs of such a large nudibranch."

However, preliminary laboratory and field observations (Waters, 1966; author's unpublished data) suggest that this is not so locally and that adult *D. frondosus* prefer thecate hydroids like *Obelia* to athecates like *Tubularia.*

The mechanism of feeding has been briefly described (Waters, 1966), and some additional information has since been obtained, particularly pertaining to predation on *Obelia commissuralis.* When the veil and lip papillae come in contact with a hydranth, the nudibranch immediately retracts these structures, and then begins to search about for the prey. This withdrawal, presumably in response to the nematocysts of the hydranth, may occur 2 to 3 times, but eventually the animal envelops the whole hydranth and, using the jaws and radula, chops it off. Occasionally the nudibranch will attack just proximal to the hydranth. In this case, it uses the same method as when the coenosarc is eaten (Waters, *op. cit.*). The nudibranch appears to use the outer lips and lip papillae to align the body and opening of the jaws parallel to the stalk. Achieving this, it grips the perisarc firmly with the outer lips, the jaws are protruded, and working transversely to the stem's long axis, they cut a hole in the perisarc. The radula is apparently extended through this hole and proceeds to rasp out the coenosarc (or the hydranth). In a relatively short time, one nudibranch is able to clean out a large hydroid colony.

There are conflicting reports about the reproductive activity of the species. Swennen (1961) reports it as being sexually mature all year except February and November, and spawning from April to August and again in January. Locally, spawn and mature animals were seen from April to October. Clark (pers. comm.) found egg masses during early May in Connecticut. Thompson (1964) and Miller (1962) indicate that *Dendronotus frondosus* may live for 2 years, breeding in both years. They also suggest that there may be more than one generation a year, but Swennen (*op. cit.*) feels that most only live one year. It is possible that a few animals do live for 2 years, not having spawned the first year, but most probably mate, spawn, and die within a year.

The nidosome is described by Hurst (1967, p. 264) as "... an untidy coil varying from pale to dark pink." I have also seen a number of white ones in relatively neat coils. There was usually only one egg per capsule, and the eggs took from 13 to 16 days to hatch.

It is hard to say how cryptic the coloration of this nudibranch is because the background may be so variable. On hydroids, it would likely not show even in its lighter brown color forms although the white, deepwater animals are quite visible to a diver. There are no other obvious means of defense although it may have some

epidermal secretions (THOMPSON, 1960b; EDMUNDS, 1966).

Dendronotus frondosus is an able swimmer, but the actual distance covered is usually small unless a current is present. Mechanical stimuli such as poking or pinching with forceps are effective in eliciting the swimming behavior. So far, no potential predator has been demonstrated to elicit swimming although VOLODCHENKO (1955) reports that this species is preyed upon by fish.

Dendronotus iris COOPER, 1863

(Plate 63, Figure 30; Text figures 4 - 6, 10 - 12)

Dendronotus iris COOPER, 1863, Proc. Calif. Acad. Nat. Sci. 3: 59

Dendronotus giganteus O'DONOGHUE, 1921, Trans. Roy. Canad. Inst. 13 (1): 187 - 190; plt. 4, fig. 47; plt. 5, figs. 57 - 59

Taxonomic Remarks

COOPER's brief description, based on color, is adequate to establish *Dendronotus iris* as a valid species name. He states (p. 59) that "this species seems more variable in color than other nudibranchiata of this coast, but I [see] no reason for considering [it] more than one species" and indicates that a slight color variation of it may be found in Puget Sound.

O'DONOGHUE (1921) recognizes that color is quite variable in the nudibranchs, even between Nanaimo, B. C. and California, but he neglects this when he describes *Dendronotus giganteus*. He makes no reference to COOPER's paper.

ODHNER (1936, pp. 1107 - 1108) recognized O'DONOGHUE's error and declared *Dendronotus giganteus* a synonym of *D. iris*. Subsequent authors, with the exception of SMITH & GORDON (1948), have retained *D. iris* as the proper name.

Body Dimensions, Texture, and Apertures

The limaciform body, the "heaviest" of all the local species of *Dendonotus,* tapers abruptly to a bluntly pointed tail. A well-rounded dorsum merges into vertical sides, the only demarcation being the 2 rows of cerata.

The largest animal found was 29.0 cm L × 6.4 cm H × 8.9 cm W and displaced 1100 cc of water. O'DONOGHUE (1921) claims a preserved specimen, measuring 21.0 cm L × 8.4 cm H × 5.5 cm W, may have been 26 cm L × 10.0 cm H × 6.5 cm W when alive. Most of the animals (many preserved) were 6.5 - 12.0 (3.0 - 29.0) cm L × 1.5 - 2.0 (0.5 - 5.0) cm H × 1.0 - 2.2 (0.5 - 4.0) cm W. A few representative animals were: 8.0 cm L × 1.5 cm H × 1.5 cm W (live); 6.5 cm L × 1.5 cm H × 1.0 cm W (live); 9.0 cm L × 3.5 cm H × 2.5 cm W (preserved); 3.0 cm L × 0.5 cm H × 0.5 cm W (preserved).

The anus is on a distinct, truncate papilla located halfway along the imaginary line joining the bases of the first and second right cerata. Often, an opaque white line marks the edge of the papilla and the plicated lips, surrounding the anal opening, are usually white.

The distinct genital openings are located about ⅔ the way up the right side, below or immediately anterior to the base of the first right ceras. Sometimes, an opaque white line marks the edge of the genital openings. Very often, in preserved specimens, the penis is extruded.

The cardiac prominence is usually not visible except as a very slight bulge. The body was smooth in all the specimens examined.

Foot

The long, quite wide foot is bluntly rounded anteriorly and terminates in a short, bluntly-rounded tail. When crawling, the foot often flares out considerably beyond the plane of the sides of the body, contrary to what MACFARLAND (1966, p. 258) says. In one 8 cm L animal, the foot was flared out 1.5 cm on either side, giving the foot a total width of 5.5 cm.

A useful, but not infallible, diagnostic character of the species is the narrow, opaque, dead-white line that edges the dorsal margin of the foot. The sole is white in the "gray" forms and a light orange in the "orange-red" forms.

The expansiveness of the foot may be an adaptation to crawling across the soft muddy bottom that this species inhabits, the greater surface area allowing for a better grip on the unstable substratum. It is almost non-functional as a grasping organ, and apparently is non-functional in helping the animal to maintain its position in a fast current (which it probably encounters only rarely in nature).

Color

Most specimens (23 of 30) were of the "gray" form, while 7 were of the "orange-red" form. In the "gray" form, the ground color varies from a clean, translucent, gray-white through yellow-brown to a dark muddy brown (Plate 63, Figure 30). The ground color is lightest on the sides, becoming darker on the dorsum and bases of the dorsal processes (cerata and rhinophores) and very dark towards the distal ends of the cerata, crown papillae, lateral papillae, and veil papillae. At the ends of the

smaller branches of these processes is a variety of colors: metallic orange (1 animal), dark purple (11 animals), a mixture of chrome-yellow and purple (9 animals) with small amounts of white found in most animals.

In the "orange-red" forms, the ground color is a beautiful "orange-red." Again, this becomes darker on the cerata, rhinophores and veil papillae, but finally gives way, at the ends of the appendages, to purple (2 animals), metallic orange (3 animals), or a mixture of the two (2 animals).

Only one animal had the white tips on the cerata with a sub-terminal orange ring described by Cooper (1863). All the intergradations between the two main color forms exist.

The lip papillae are normally tipped with chrome yellow or are unpigmented, but 2 specimens had metallic orange in place of the yellow.

Cerata

There are 4 - 6 (3 - 8) pairs of stout, but very tall and dendriform cerata, the last pair being about half as tall as the first. Arranged at decreasing intervals on the dorsolateral margins of the body, they begin about $\frac{1}{3}$ of the way back from the anterior end. Nearly all the specimens have 2 (1 - 4) small, branched, unpaired papillae on the posterior end.

The cerata are not firm and erect as they are in the less dendritic forms, but are instead quite supple and extensible. Because of these traits, and the fact that they are usually badly mutilated in the dredge hauls, it is often difficult to determine the number of main branches in a ceras.

The very thick, basal portion of the ceras divides almost immediately to give rise to a number of tall, thick main branches arranged in a "fan-shaped" pattern (Figure 4a). There are 3 (2 - 5) main branches in the first pair (no. 1), 3 (2 - 4) in no. 2, 2 - 3 in no. 3, 2 (1 - 3) in no. 4, 1 (1 - 3) in no. 5, 1 (0 - 2) in no. 6, and 1 in nos. 7 and 8. These subdivide into secondary branches that may be nearly as long as the main ones while the tertiary branches are only slightly shorter. The secondary and tertiary branches end in small, delicate tufts, giving the animal a very bushy appearance when viewed from above. The medial branch is the longest (up to 5 - 7 cm in a 15 cm L animal) while the lateral is the shortest.

According to MacFarland (1966) only the first pair of cerata and the rhinophores have "ceratal cores" or hepatic diverticula, arising from the anterior lobes of the liver. Odhner (1936) states that the diverticula are ramified throughout the cerata as shown by Alder & Hancock (1845), but neglects to mention in how many pairs this occurs. In 10 animals examined, I always found the situation described by MacFarland.

Rhinophore and Clavus

The rhinophore resembles the cerata with its very thick stalk and the extensive branching of the lateral and crown papillae. At the base, the lateral papilla is thick but it soon divides into a number of smaller secondary branches which in turn branch and terminate in small, delicate tufts. Arranged vertically on the posterior border of the rhinophore stalk are 4 (2 - 6) small, branched papillae found only in this species.

The inconspicuous, muddy brown, conical clavus is perfoliated with about 25 (15 - 31) leaves alternating in breadth. The top 2 - 4 and bottom 4 - 6 leaves are usually small and equal. Those inbetween alternate more or less regularly with the wider leaves almost completely covering the narrower ones.

The 5 (2 - 5) crown papillae are relatively longer and more branched than in most species except *Dendronotus rufus*. The branching is not as neat as in *D. rufus* but tends to occur at any point from the base to the tip, making it hard to ascertain the actual number of crown papillae in many cases. The postero-medial is the longest, being 2 - 4× longer than the 3 almost equal, anterior papillae. The postero-lateral may be from $1\frac{1}{2}$ - 3× longer than the anterior papillae.

Head, Lips, and Veil

On the indistinct veil, there are almost always 3 (2 - 4) pairs of stout veil papillae varying considerably in size and degree of branching. However, they are generally sparsely branched and short, relative to the animal's size.

Contrary to what MacFarland (1966) shows in his drawing compiled from a number of specimens, I found that the medial pair was usually smallest and the lateral pair (no. 3) the largest (from $1\frac{1}{2}$ o 2× longer than no. 1). Pair no. 3 is divided almost from the base into a smaller, sparsely branched lateral ramus and a much longer (2×), more branched medial ramus. Often, the veil papillae were all very small and simple, making them indistinguishable from the lip papillae except by position.

There are many lip papillae (20 - 40, depending on the size of the specimen) arranged in 3 - 4 irregularly crescentic rows around the mouth and lips. The most anterior row, immediately ventral to the veil papillae, consists of 6 (5 - 8) simple to slightly branched papillae about equal in length to the shortest veil papillae. In the second row, there are 7 (6 - 12) simple papillae about $\frac{1}{2}$ to $\frac{2}{3}$

the size of the preceding ones. The most ventral "row" of 10 - 25 small, simple papillae and tubercles is very irregularly arranged around the mouth.

Jaws

The jaws of *Dendronotus iris* (Figure 10) are the largest and heaviest seen in any of the local species of *Dendronotus*. In the whole genus, only *D. robustus* may have heavier, albeit relatively shorter, jaws. MacFarland (1966) found in a 9.1 cm L preserved specimen that the jaws were 1.72 cm L × 0.75 cm W (see Figure 5 for measurements). In 5 specimens that I examined, the sizes were:

Dendronotus iris

length of animal	length of jaw	height of jaw	width of jaw
	(measurements in centimeters)		
13.0	2.8	0.95	0.85
7.0	1.5	0.65	
8.0	1.6	0.65	
10.0	1.8	0.70	
4.0	1.1	0.35	

The total length of the animal body is only about 5× that of the jaw.

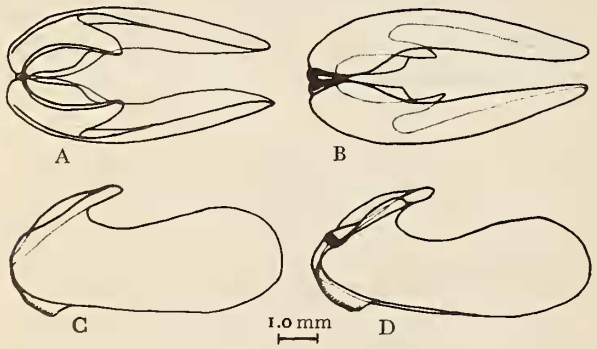

Figure 10

Dendronotus iris jaw
A. Dorsal view B. Ventral view C. Inside lateral view
D. Outside lateral view

The jaws are a deep reddish brown on the masticatory process and hinge, fading to a light yellow along the dorsal process and body. The masticatory denticles may be almost black.

The body of the jaw is an elongate, mytiloid shape, widest at the posterior end. The length of the body is slightly less than 3× the maximum width which occurs in the posterior third. The strong dorsal process, weakly curved, is inclined posteriorly at about 40° to the longitudinal axis of the body, and is joined to the body by a strong, convex expansion for over half of the length of the process. The dorsal process is about a third (or slightly more) as long as the body. The strong, arched masticatory process is joined to the body by another thick, but weakly concave expansion. There are about 85 - 100 large denticles on the masticatory border.

A feature not seen in any other *Dendronotus* is the very long, convoluted esophagus. Its function is not known at present, although it may be related to the fact that the animal can extrude the whole buccal mass through the lips when feeding (moribund animals usually extrude the "proboscis").

For a more complete description of the jaw, the reader is referred to MacFarland (1966, pp. 259 - 260).

Radula

The radula (Figure 11) is most unlike that of any other *Dendronotus*. The radula formula, according to MacFarland (1966) and O'Donoghue (1921) is:
34 - 46 (11 - 20 · 1 · 11 - 20) and 35 - 40 (12 - 16 · 1 · 12 - 16), respectively. In 9 specimens, I found it to be:
41 - 61 (11 - 21 · 1 · 11 - 21), giving a maximum range of 34 - 61 (11 - 21 · 1 · 11 - 21).

The tall sharp-pointed cusp of the medial tooth is only slightly higher than wide (Figure 6) and bears on the concave margins 11 (9 - 18) strongly developed, pointed denticles. These denticles, more prominent than in any other species, are slightly concave on the medial edge. The lateral margin of the denticle continues anteriorly on the tooth as a deep furrow. Toward the apex of the cusp, particularly on teeth from the posterior half of the radula, the denticles decrease in size, number, and regularity. For example, in one radula with 58 teeth, there were 7 large, regularly spaced denticles on the first medial tooth,

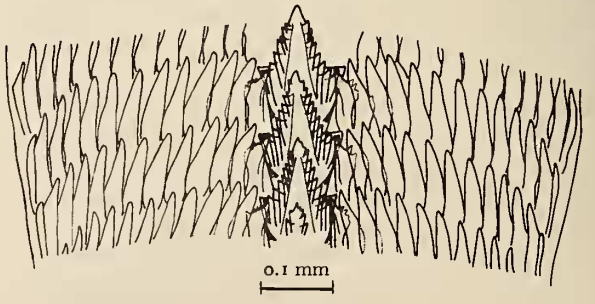

Figure 11

Dendronotus iris radula
Rows 22 to 24 in a radula with 43 rows of teeth

9 on the 25th, 12 on the 35th and only 8 irregular ones on the 52nd.

The lateral teeth become more numerous from the oldest rows to the youngest. The oldest 1 - 3 rows have no lateral teeth, rows 2 - 5 have 3 - 10 teeth, and by about row 8, the main battery of teeth is present with only 1 - 3 more to be added toward the posterior end. Usually, there are no denticles on the laterals but occasionally, the no. 1 tooth in the first 10 - 15 rows will be serrulated or even bear 1 - 8 short, sharp denticles. Rarely, the no. 2 lateral in the first few rows will also be serrulated or bear a few tiny denticles.

The typical lateral tooth consists of a flat, elongated base upon which there is a gently tapering, blunt-pointed, stout cusp inclined at about 20° toward the midline of the radula. The outermost 3 - 4 lateral teeth decrease in size, the most lateral one being a narrow, flat plate with a short spine. The innermost lateral has a rod-like base that terminates in a short, stout cusp.

Reproductive System

The thin hermaphrodite duct joins the large, white, lobulated hermaphrodite gland to the very long, tortuous ampulla which is relatively the longest found in the genus (Figure 12). The ampulla merges indistinctly with the spermoviduct which bifurcates, giving rise to a short proximal portion of the vas deferens and relatively long, thin-walled, almost transparent oviduct.

The prostate is made up of alveoli surrounding and concealing more than ¾ of the total length of the looped vas deferens. The short, narrow, muscular distal portion of the vas deferens enters the base of the penis where it continues as the coiled ejaculatory duct. The long penis, sheathed in a relatively thick-walled preputium, is very thick throughout its whole length; it is the largest in the genus.

The short, wide, muscular vagina terminates in an indistinct, somewhat irregularly shaped seminal receptacle. Located on the distal third of the vagina is the bursa copulatrix atop a very long, thin stalk. A long, convoluted insemination duct, much narrower than the vagina, joins the seminal receptacle to the fertilization chamber via the oviduct.

Odhner (1936, figure 40), in a poor diagram of the *Dendronotus iris* genital system, has misplaced the insemination duct, a continuation of what he calls the vesicula seminalis (v.s.), and the spermoviduct, a continuation of what he calls the ampulla (f.). The spermoviduct should terminate between the prostate and the insemination duct.

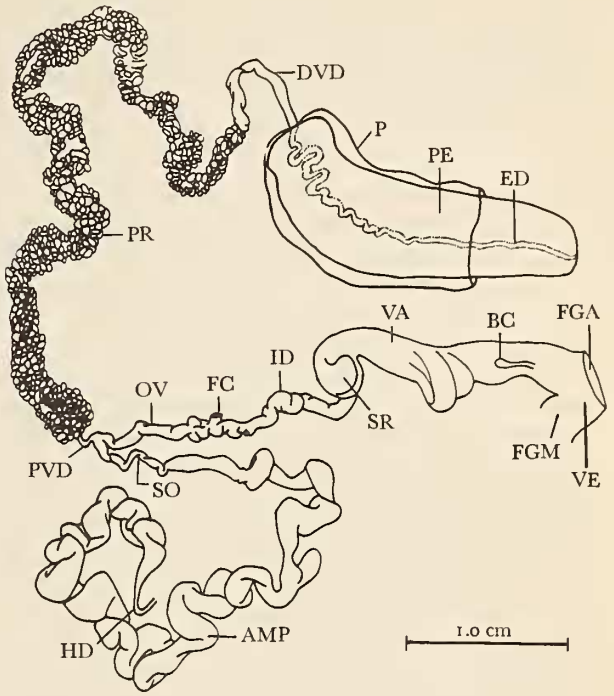

Figure 12

Reproductive system of *Dendronotus iris* (exploded view)
AMP = ampulla BC = bursa copulatrix
DVD = distal vas deferens ED = ejaculatory duct
FC = fertilization chamber FGA = female genital aperture
FGM = (to) female gland mass HD = hermaphrodite duct
ID = insemination duct OV = oviduct P = preputium
PE = penis PR = prostate PVD = proximal vas deferens
SO = spermoviduct SR = seminal receptacle VA = vagina
VE = vestibule

Geographical Distribution

Dendronotus iris has usually been collected subtidally from 7 m at Nanaimo, B. C. to about 200 m off Unalaska in the Aleutian Islands. The southern limit at present is the Coronados Islands in Mexico (Lance, pers. comm.). It has been recorded from Nanaimo, B. C. (O'Donoghue, 1921); the Queen Charlotte Islands, B. C. (D. B. Quayle, pers. comm.); Puget Sound (Cooper, 1863); and numerous areas in California (Smith & Gordon, 1948; G. E. MacGinitie, pers. comm.). Agersborg (1922) reports one from the shore of Shaw Island and another from logs near the Puget Sound Biological Station, both in the San Juan Archipelago.

Ecology

This species has been obtained by dredging in a number of places around the San Juan Islands (see Materials and Methods, above) where it is apparently present year round. I collected 15 more while SCUBA diving at Nanaimo.

The animals are almost always collected from muddy bottoms where there is little current action. This type of bottom often supports a dense population of *Cerianthus* sp., the burrowing anthozoan that is the principal food of *Dendronotus iris*; in fact, the available evidence would suggest that it is the sole food of this nudibranch.

Dendronotus iris displays a specialized feeding behavior. How it locates the *Cerianthus* is unknown, but, upon contact with the anemone's tube (which extends as much as 15 cm above the substratum), *D. iris* begins to crawl up the tube. The veil papillae are extended and the head moves slowly back and forth through about a 120° arc. When *D. iris* contacts a *Cerianthus* tentacle, the nudibranch immediately withdraws. Again the veil papillae are extended and the head moves back and forth in ever decreasing arcs until *D. iris* has "homed in" on the tentacle. *Dendronotus iris* then lifts the anterior third of the body free of the tube, lunges forward, at the same time extruding the buccal mass through and past the mouth. The *Cerianthus* tentacles are grasped with the jaws and chopped off whole by the radula. This attack must be and is done rapidly as the *Cerianthus* is able to withdraw quickly. Withdrawal seems to be a poor defense; smaller *D. iris* apparently can climb down the tube or are pulled down the tube when the attacked *Cerianthus* retracts.

I have found whole, undigested *Cerianthus* tentacles in the stomachs of many specimens as well as multitudes of nematocysts in the intestine and fecal pellets; no other prey species were found. MacFarland (1922) reports finding fragments of a nemertean in one animal. Agersborg (1922) tried to feed many things to a *Dendronotus giganteus* (= *D. iris*), but it was only interested in the tentacles from an unnamed coelenterate which were mouthed, but not eaten.

Very little information is available concerning reproduction in *Dendronotus iris*. In the laboratory, between February 7 and 13, 1967, 3 white egg masses were deposited in a large rounded bundle. There were 45 - 50 and 31 - 40 eggs per capsule. The veligers hatched after 13 - 15, 16, and 17 days from the 3 egg masses. In June, 1967, 3 more egg masses with up to 100 eggs per capsule were laid by 3 very large animals (28.7, 25.4, and 20.3 cm L). The same animals were copulating and laying eggs when collected at Clarke Rock, Nanaimo. In June, 1968, 8 egg masses were seen on the tubes of *Cerianthus* sp. at the Monterey Breakwater, Monterey, California.

There is some suggestion that this species, particularly the gray form, is cryptic in its natural habitat although first-hand observation indicates that it can be spotted fairly easily by a diver. Predators, probably fish, must occasionally detect *Dendronotus iris*, either by sight or smell, and attempt to eat the nudibranch. Evidence for this is found in the numerous *D. iris* collected with parts of the dorsal appendages missing.

The cerata (or portions thereof) are rather easily broken off with rough handling. Upon severance, these parts move quite naturally and even "swim" to some degree. This may be a protective measure, serving as a decoy while the nudibranch makes its escape.

Agersborg (1922) states that *Dendronotus iris* is a very capable swimmer and suggests that it is basically pelagic, creeping on the bottom only occasionally. I suggest that the opposite is more likely in view of the extensive development and size of the foot as a creeping organ, and the nudibranch's food preference. It swims quite readily in the laboratory or field when disturbed, and has occasionally been seen to swim with no apparent provocation. The swimming appears to be directed upwards, presumably away from disturbing factors on the bottom. That this swimming is very effective is supported by the sightings of animals on the surface over 130 m of water and about half a mile from shore in Saanich Inlet.

Dendronotus robustus Verrill, 1870

Dendronotus robustus Verrill, 1870, Amer. Journ. Sci. Arts 50: 405 - 406; fig. 1
Dendronotus velifer Sars, 1878, Bidr. Kundsk. Norg. Arktisk. Fauna, pp. 238 - 239, plt. 28, fig. 2

Taxonomic Remarks

There has been little doubt expressed by previous authors (Bergh, 1894; Odhner, 1936) that *Dendronotus robustus* is a distinct and valid species. Verrill's description is complete enough to prevent confusion and for this reason it is difficult to understand why Sars (1878) redescribed it under a different name.

I have seen no living or preserved material of this species, so the description is compiled from the literature, using the two above references plus Bergh (1894). These descriptions are not very complete nor are they specific in detail.

Body Dimensions, Texture, and Apertures

The body is stouter, less compressed laterally and less acutely tapered posteriorly than is *Dendronotus frondosus* (see plate 28, fig. 2 in Sars, 1878). The largest animal

observed was about 9 cm long (Bergh, 1894), but measured ones were 2.5 cm L × 1.25 cm W × 1.25 cm H (live) (Verrill, 1870) and 2.8 cm L × 1.0 cm H × 0.95 cm W (preserved) (Bergh, 1894). Verrill (1879, 1882) claims to have found some larger animals, but he gives no dimensions.

The anus, atop the anal papilla, is located nearer the second right ceras than is true for other species. The genital openings are "as usual" (Bergh, 1894).

Apparently there is no cardiac prominence. Bergh (1894) notes that the body is smooth, but Sars' figures (1878) show a scattering of small tubercles all over the dorsal surface.

Foot

The foot is as wide as the body (Verrill, 1870) and small objects like hydroids can apparently be grasped by infolding the edge of the foot.

Color

Verrill (1870) claims the animal is a pale grayish ground color liberally sprinkled with small yellow spots except on the veil papillae and rhinophore stalk where there are only a few spots. Sars (1878) and Bergh (1894) mention a reddish body seeded with white spots. All the lip and veil papillae are tipped with a sulphur yellow (Verrill, *op. cit.*).

Cerata

There are 6 - 7 pairs of relatively short, stout cerata. They are not exceptionally arborescent, most of the branching being only short, thick offshoots. In the first to third pairs of cerata, the main lateral branch arises independently of and lateral to the base of the other main branches. In pairs 4 and 5, the lateral branch arises from the base of the ceras, while all the posterior pairs are only single stalks.

Rhinophore and Clavus

There is no lateral papilla on the stout, round rhinophore stalk. The perfoliate clavus, with 10 - 12 (Verrill, 1870) or 15 - 20 (Bergh, 1894) leaves is surrounded by 5 simple, round, smooth, tapering crown papillae of which the posterior 2 are the longest.

Head, Lips, and Veil

The head is covered over by an enormous veil, upon which there are 8 - 10 veil papillae. The outer two on each side are the largest by about 2×, but they are all knob-like with short, simple branches on the ventral side.

About 10 small, unequally sized lip papillae adorn each side of the lips. Some are forked, but most are simple.

Jaws

The jaw, relatively shorter than is common for *Dendronotus,* is also thicker and heavier than is usual for the genus. No other information or diagrams have been published.

Radula

The radula formula is 29 - 35(15 - 21 · 1 · 15 - 21). Bergh (1894) states that the median teeth of the radula are horn yellow while the lateral teeth are colorless.

The median tooth is strongly denticulated, especially proximally, with 15 - 20 sharp denticles that become shorter towards the tip of the cusp (see plt. 2, figs. 7 - 9, Bergh, 1894).

The hook of the lateral tooth becomes longer and more curved from the inside toward the middle and then begins to decrease in size as the outermost teeth are approached. The innermost tooth (no. 1) has no denticles and virtually no cusp. Teeth no. 2 - 4 have 1 - 2 strong denticles at the base of the cusp. Most of the other laterals, save the outer 1 - 3, have 3 - 5 smaller denticles at the base of the long cusp although the denticulation is irregular and often absent. The outermost laterals are without denticles and have only a small cusp.

Reproductive System

There is virtually no description of this system in the literature. Odhner (1936) mentions that the seminal receptacle is a pouch-like structure off the proximal end of the vagina and that the prostate is a single ring of about 11 vesicles.

Geographical Distribution

So far, this species has only been found in the Arctic and Atlantic Oceans, and has been reported from Spitzbergen, Greenland, Siberia, northern Norway (Odhner, 1926) and from Cape Cod to Nova Scotia (Verrill, 1879).

Ecology

There are no published data concerning any aspect of ecology except that *Dendronous robustus* occurs from the intertidal down to at least 200 m (Odhner, 1939).

Dendronotus dalli BERGH, 1879

(Plate 63, Figure 31; Text figures 1, 4 - 6, 13 - 15)

Dendronotus dalli BERGH, 1879, Proc. Acad. Nat. Sci. Philadelphia 5 (1): 150; plt. 1, fig. 21; plt. 2, figs. 9 - 12; plt. 3, figs. 2 - 6

Dendronotus elegans VERRILL, 1880, Proc. U. S. Nat. Mus. 3: 385 - 386

Dendronotus frondosus (ASCANIUS, 1774). ODHNER, 1936, Mém. Musée Roy. Hist. Nat. Belg., ser. 2, 12 (3): 1105 - 1109

Taxonomic Remarks

BERGH (1879) first described *Dendronotus dalli* from a "bulbus pharyngeus" or buccal mass dredged in the Bering Strait. The main points of difference from *D. frondosus,* he felt, were the complete lack of denticulation on the median tooth and the more distinct denticles on the masticatory border of the jaw.

In a later paper that included a more extensive description of a whole animal, BERGH (1894) expressed some doubt about the validity of *Dendronotus dalli.* He indicated that it, like *D. purpureus,* may be a color variety of *D. frondosus* that lacks all the median tooth denticulation. However, he retained the name *D. dalli* in a still later description of a specimen collected at Bear Island (BERGH, 1900).

O'DONOGHUE (1921) gave a brief description of the external characters of a small specimen. However, this description, with the exception of the larger number of lateral teeth, fits *Dendronotus* spec. nov. almost exactly. O'DONOGHUE deposited the specimens, upon which he based his description, in the museum at the Nanaimo Biological Station, but during a subsequent move, they were apparently lost (Clarke, pers. comm.; Quayle, pers. comm.).

ODHNER (1936) expressed some doubt about O'DONOGHUE's description and concluded that, without more specific and detailed information, *Dendronotus dalli* should be considered a synonym of *D. frondosus.* He dismissed all of BERGH's work by stating that the radula characters upon which BERGH based his descriptions are too variable for taxonomic purposes (ODHNER, 1926, 1936). MACFARLAND (1966, p. 257), in agreeing with ODHNER, stated:

> "He [O'DONOGHUE] gives no anatomical details to support his conclusion [that *Dendronotus dalli* is a distinct species], and until these are produced, the conclusion of ODHNER (1936) that the radula characteristics are too variable to justify species discrimination are most reasonable."

VERRILL's (1880) description of *Dendronotus elegans* strongly suggests that the animal was a *D. dalli* and not a morphological variant of *D. frondosus* as ODHNER (1936) suggests. Because there are no further records published by VERRILL, I suggest, on the basis of this description, that *D. elegans* be considered a synonym of *D. dalli.*

The following description shows that *Dendronotus dalli* is indeed a valid species, distinct morphologically and biologically from *D. frondosus.*

Body Dimensions, Texture, and Apertures

In the relatively heavy, laterally compressed, limaciform body, the rounded dorsum merges indistinctly with the vertical sides. The posterior third of the body tapers to form a short, moderately blunt-pointed tail (Figure 1).

The largest specimen was 13.5 cm L and there were 11 others over 9.0 cm L. Most of the animals were 4.0 - 6.0 (1.9 - 13.5) cm L × 0.7 - 1.5 (0.6 - 3.1) cm H × 0.5 - 1.0 (0.4 - 1.6) cm W. A few representative measurements of live animals were: 4.4 cm L × 0.7 cm H × 0.5 cm W; 6.5 cm L × 1.2 cm H × 0.9 cm W; 8.0 cm L × 1.5 cm H × 1.2 cm W. BERGH (1879, 1894) estimates one animal to be 10 cm L while others were 3.5 cm and 4.2 cm L, both preserved. O'DONOGHUE's (1921) largest specimen, preserved, was 3.1 cm L × 0.9 cm H × 0.6 cm W. VOLODCHENKO (1955) reports specimens up to 10 cm L.

The anal papilla, if present, is inconspicuously located halfway beween the bases of no. 1 and no. 2 right cerata.

The conspicuous genital openings are located about halfway up the right side of the body, just anterior to the first ceras.

The cardiac prominence is usually only a slight elevation, but in a few specimens it is protruded up to 4 - 5 mm above the dorsum. Only 2 of 60 animals had any body papillae and these were limited to the cardiac prominence. All the other animals were smooth.

Explanation of Plate 63

Figure 29: *Dendronotus frondosus* (ASCANIUS), white form from 20 m off San Juan Island, Washington × 2

Figure 30: *Dendronotus iris* COOPER, grey form. In this particular animal, the grey is overlaid with the muddy brown pigment commonly seen on animals from deep-water muddy bottoms × ½

Figure 31: *Dendronotus dalli* BERGH. Note the relatively short, stout, but extensively branched cerata (CE) and veil papillae (VP) × 1

Figure 32: *Dendronotus rufus* O'DONOGHUE. Note the tall, extensively branched cerata (CE) and rhinophores (RH). The magenta pigment is less dense on the veil papillae (VP) and rhinophores × ½

Figure 29

Figure 31

Figure 32

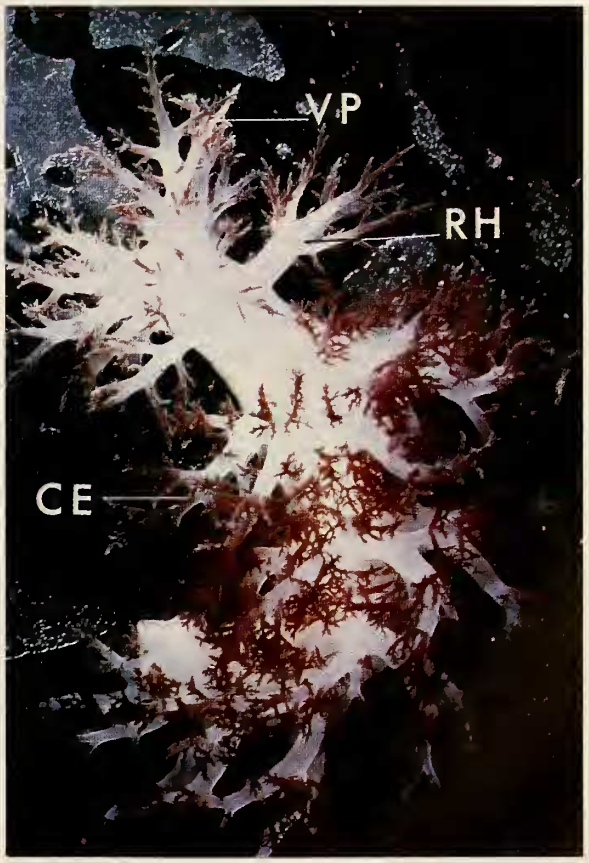

Figure 30

Foot

The foot (Figure 1) is about $\frac{1}{8}$ as wide as long. The anterior end is blunt and rounded while the posterior end tapers abruptly to a blunt point. When the animal is crawling, the foot flares laterally along its whole length though not as extensively as in *Dendronotus iris*. During swimming, the edges fold quite tightly together. The sole of the foot is white or very pale pink with a faint hint of darker pink around the edges; this edging is not as prominent as it is in *D. iris* or *D. rufus*.

Despite the large size of the foot, the animal is capable of clinging stubbornly to the stiff branches of the hydroids, *Abietinaria rigida* or *A. amphora*. It is able to maintain its position on plain rock in the face of a relatively fast current.

Color

Previously, all the descriptions have been of preserved specimens which become a dull, indifferent gray in alcohol or formalin. In life, *Dendronotus dalli* is rather uniformly colored in varying shades of translucent white through pearl pink to salmon pink; 3 specimens were a mauve hue. Most of the animals collected were pearl pink (Plate 63, Figure 31). The color is lightest on the sides, becoming darker on the dorsum and darkest on the cerata, rhinophores, and veil papillae. The extremities of these processes are usually covered with an opaque, dead-white pigment, occasionally extending down the main branches in irregular lines of scattered patches. A few animals were sparsely to liberally sprinkled with tiny, opaque, white spots.

The clavus and oral region (outer lips and lip papillae) are a yellowish color. The tan to dark pink liver and the white gonad are plainly visible through the body wall.

Cerata

The short, but extensively branched cerata are in 6 - 7 (4 - 8) pairs arranged at intervals along the dorso-lateral margin of the body. Volodchenko (1955) reports up to 9 pairs. Both the interval and size of the cerata gradually decrease from anterior to posterior. On the tail, there are 1 - 2 (1 - 5) unpaired, but often relatively large, branched processes or "accessory cerata." These occasionally occur between the other cerata also.

The main branches are quite stout, but short; often the total height of the cerata is not much more than the height of the body. The main branches give rise to even shorter, stout secondary branches which in turn may divide into small tertiary branches. These secondary and tertiary branches, because they are short and arise from all sides of the main branches, impart a "fuzzy" appearance to the cerata. When viewed from above, the ceratal mat provides very little cover for the dorsum.

The branching pattern is "fan-shaped" (Figure 4a) with 4 (3 - 4) main branches in no. 1 cerata, 3 - 4 in no. 2, 3 (2 - 4) in no. 3, 3 (2 - 3) in no. 4, 2 - 3 in no. 5, 2 (1 - 2) in no. 6, and 1 in nos. 7 and 8. Where there are 4 main branches, there is a dichotomy at or very near the base of the ceras. Each of these stalks divides almost immediately to form 4 branches. The medial branch is short, the next one out (no. 2) is the longest, no. 3 is about equal to no. 2 and the lateral branch (no. 4) is shortest, being about $\frac{1}{2}$ to $\frac{1}{3}$ as long as no. 3. Where there are 3 main branches, the lateral branch (no. 3) arises at or near the base of the ceras above which the ceras bifurcates to form branches no. 1 and no. 2. The medial branch is the longest, but no. 2 is only slightly shorter while the lateral is again about $\frac{1}{2}$ to $\frac{1}{3}$ as long as no. 1. If there are only 2 main branches, they divide at the base and no. 2 is variable in length. In some large specimens, there is an extra medial branch in the first pair of cerata.

The cerata of *Dendronotus dalli* appear to be subject to many aberrations in size and branching. This may be the result of attacks by predators, probably fish.

Rhinophore and Clavus

The rhinophore, like the cerata, is relatively short and stout with many small branches.

The lateral papilla, arising from or near the base of the rhinophore stalk, is heavy and long, often reaching higher than the extended clavus. The degree of branching varies a good deal from a few small, simple papillae arising from the main branch to the extensive secondary and tertiary branching comparable to the cerata.

The yellow, perfoliate clavus has 20 - 24 (16 - 33) roughly alternating, shallow-cut leaves. The top 3 - 4 and bottom 2 - 3 leaves are small and equal. The large leaves almost completely encircle the clavus while the small ones are limited to the posterior border.

Extending upward from the rhinophore sheath are 5 (4 - 12) highly variable crown papillae. They are usually long, but not particularly stout. All are about equal in length though the posterior two may be 2 ×longer than the others, and often as tall as the rhinophore stalk itself. The branching consists of a few relatively short papillae arising from the proximal half of the main stalk.

Head, Lips, and Veil

The veil, not sharply marked off from the head, bears 4 or, more often, 5 pairs of stout, extensively branched veil

papillae radiating fan-like from it (Figure 1). The arrangement and size of the veil papillae varies, making it difficult to count and describe them. In those animals with 4 pairs of papillae, the medial pair (no. 1) is usually the longest, no. 2 is about $\frac{1}{2}$ to $\frac{2}{3}$ as long as no. 1, no. 3 is about equal to no. 1, and no. 4 is the shortest at a $\frac{1}{4}$ to $\frac{1}{2}$ the length of no. 1. When 5 pairs are present, no. 1 is the longest. No. 2 pair may be $\frac{1}{4}$ to $\frac{1}{5}$ as long and originates ventro-lateral to no. 1. Or, it may be about equal to no. 3 in size. Pairs no. 3 and no. 4 are usually about $\frac{1}{2}$ to $\frac{3}{4}$ as long as no. 1. The unbranched lateral pair, no. 5, is about $\frac{1}{4}$ to $\frac{1}{5}$ as long as no. 1. In a few specimens all 4 or 5 pairs of veil papillae are approximately the same length.

Many (15 - 30+) simple lip papillae, ranging in length from mere tubercles near the mouth to long, finger-like papillae on the lateral margins, adorn the oral surface (Figure 1). Some of the larger lip papillae, especially those just ventral to the veil papillae, may be forked at the tip or, rarely, they may be quite bushy. All the lip papillae are sensitive and able to retract when disturbed.

Jaws

The jaws of *Dendronotus dalli* (Figure 13) seem longer and stronger than they are. The buccal mass has a length : width ratio of 1.2 - 1.4 and a length : height ratio of 1.5 - 1.7.

The jaws are transparent, citron yellow, slightly darker on the hinge and masticatory process. In his original description, Bergh (1879) incorrectly states that the jaw is darker than that of *Dendronotus frondosus,* but in subsequent papers (1894, 1900), he indirectly corrects this error.

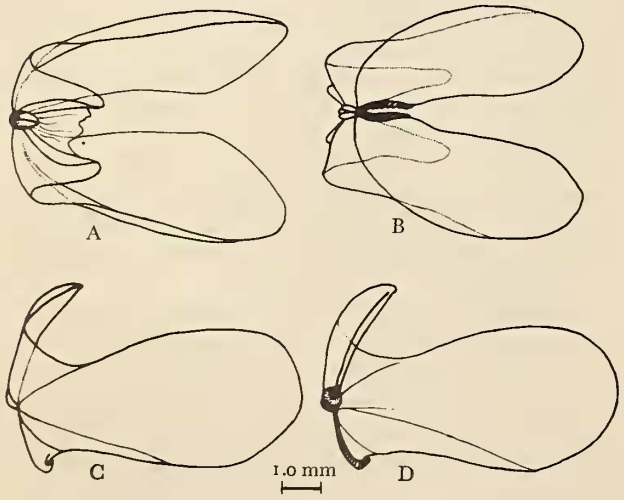

Figure 13

Dendronotus dalli jaw

A. Dorsal view B. Ventral view C. Inside lateral view D. Outside lateral view

The body has a deeply convex, mytiloid form, widest in the posterior third and bluntly convex on the posterior end. The length : width ratio is about 2 : 1 (Figure 5 for measurements). The large, strong, deeply grooved dorsal process, about 0.45× the jaw body length, is inclined at a 60° angle to the longitudinal axis of the jaw body. The process is joined to the body by a strongly convex expansion for less than half of its length. The short masticatory process, only slightly arched, bears about 200 low denticles (Bergh, 1894) and is joined to the body by a thick, slightly concave expansion.

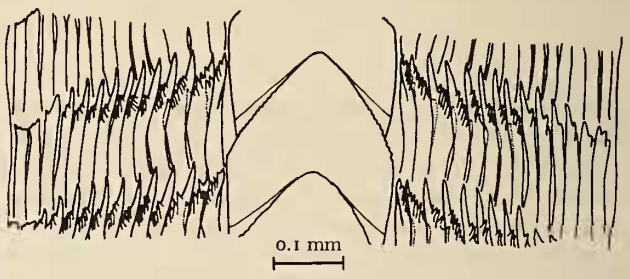

Figure 14

Dendronotus dalli radula
Row 21 in a radula with 38 rows of teeth

Radula

The radula (Figure 14), Odhner's (1926, 1936) comments notwithstanding, is distinctly different from that of *Dendronotus frondosus.* When the figures from all his descriptions are compiled, Bergh (1879, 1894, 1900) reported a radula formula of 42 - 51 (11 - 16 · 1 · 11 - 16) for *D. dalli.* O'Donoghue (1921) found it to be 38 - 40 (10 - 14 · 1 · 10 - 14). From a study of 29 radulae, I obtained a radula formula of 37 - 48 (9 - 14 · 1 · 9 - 14). The composite formula is 37 - 51 (9 - 16 · 1 · 9 - 16).

Bergh (1894) stated that the median teeth are a dark mahogany color but I found only clear or very slightly yellow teeth in fresh specimens.

The cusp of the median tooth, rounded at the apex and weakly concave on the sides, becomes taller towards the radula sheath. In the oldest teeth the width : height ratio of the cusp is about 2 : 1, whereas from about row no. 20 on it is 1.7 - 1.9 : 1 (Figure 6 for measurements). As maintained by Bergh (1879, 1894) and O'Donoghue (1921), there are no conspicuous denticles on the median teeth. Except for a few cases, there is only an indistinct,

irregular serrulation at most and this disappears toward the apex. A few specimens had 30 - 40 tiny, distinct, regularly arranged denticles on each side of the cusp, usually in the posterior half of the radula.

The lateral teeth are long, narrow, flat plates increasing in size from anterior to posterior. The cusps of the lateral teeth are slightly inclined (about 10°) toward the midline and away from the long axis of the tooth's base. On the innermost laterals, the cusp is about equal in length to the denticles. The next 2 - 4 teeth have large, sharp, weakly curved cusps bearing denticles along the proximal, lateral border. The sharp, thin cusps on the outer teeth decrease in length and finally disappear from the outer 1 - 2 teeth.

Of the 9 - 14 lateral teeth in the specimens I examined, only the outer 2 - 3 (1 - 5) were without denticles. All the rest have 3 - 7 (1 - 19) sharp, irregularly arranged and shaped denticles that are long and heavy when there are only a few (1 - 6), but more slender when there are many (7 - 11+). There is a tendency for the number of denticles to decrease from the inner to the outer teeth. On the inner two laterals (no. 1 and no. 2), there are respectively, 4 - 5 (2 - 11) and 4 - 6 (2 - 10) denticles. There are 4 - 6 (3 - 11) denticles on no. 3, 3 - 6 (2 - 10) on no. 4, 3 - 5 (2 - 8) on no. 5, 2 - 4 (1 - 8) on no. 6, 1 - 4 on no. 7, 1 - 3 on no. 8 and no. 9, and sometimes 1 or 2 small ones on no. 10. Numbers 8 to 10 occasionally lack any denticles.

Reproductive System

In Figure 15, the reproductive system is spread out to show the relative size and relationships of the component parts.

Each lobule of the hermaphrodite gland seems to have a dark gray patch on the distal end. The hermaphrodite duct links the gland to the relatively long, narrow, coiled ampulla which merges indistinctly into the short, wide spermoviduct. The short proximal portion of the vas deferens expands into the prostate consisting of many small, usually spherical alveoli arranged as a flattened sphere concentric with the vas deferens. The wide, quite short and muscular distal portion of the vas deferens tapers very slightly before entering the penis. The penis is bullet-shaped, thick at the base and tapered to a point in the distal third.

The short, wide vagina narrows slightly before entering the vestibule relatively far from the common female genital opening. The small bursa copulatrix opens into the vagina near its distal opening. The seminal receptacle, a flattened ovoid structure that is bent back on itself, is located at the proximal end of the vagina. The insemination duct appears to enter the vagina about halfway between the bursa copulatrix and the seminal receptacle,

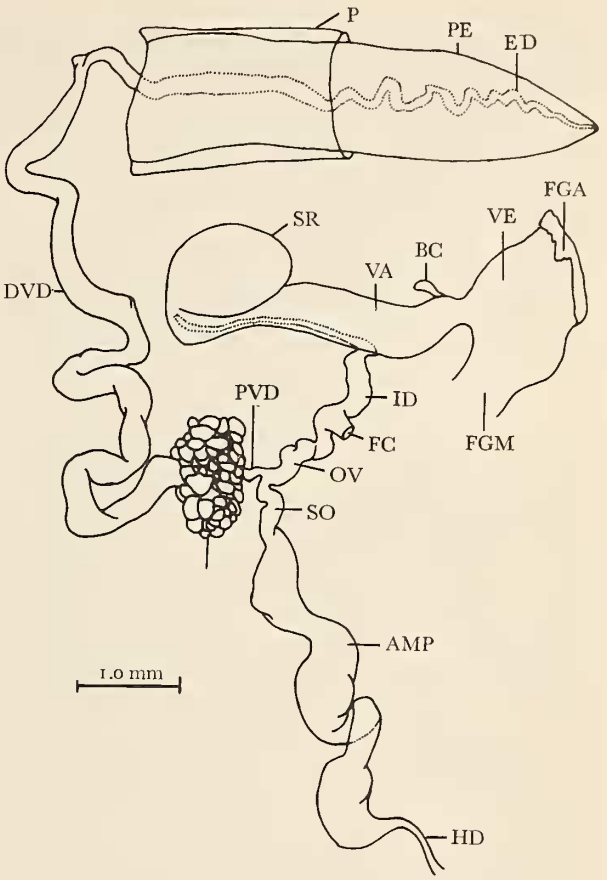

Figure 15

Reproductive system of *Dendronotus dalli* (exploded view)
AMP = ampulla BC = bursa copulatrix
DVD = distal vas deferens ED = ejaculatory duct
FC = (to) fertilization chamber FGA = female genital aperture
FGM = (to) female gland mass HD = hermaphrodite duct
ID = insemination duct OV = oviduct P = preputium
PE = penis PR = prostate PVD = proximal vas deferens
SO = spermoviduct SR = seminal receptacle VA = vagina
VE = vestibule

but closer inspection reveals that it continues as a tube within the lumen of the vagina and actually opens near the mouth of the seminal receptacle. The other end of the insemination duct is confluent with the short, transparent oviduct forming a fertilization chamber.

Geographical Distribution

Except for one specimen, this species has only been collected in the northeastern Pacific and the Bering Straits

at depths of 10 - 60 fathoms. Bergh (1879, 1894, 1900) had specimens from Bear Island in the Barents Sea (1), the North Pacific (2), and Bering Strait (1). O'Donoghue (1921) collected them at Halibut Bank, Nanoose Bay, and Gabriola Pass, all off eastern Vancouver Island, B. C. Volodchenko (1955) mentioned them as occurring in the North Pacific off the Russian Coast.

Besides the Victoria Breakwater (50 animals), I collected them from Albert Head, Victoria (3), Eagle Point (6), Lonesome Cove (5), Harney Channel (4 dredged), Turn Rock (3), and San Juan Channel (4). The latter 5 areas are in the San Juan Archipelago (see Appendix I).

Ecology

Up to now, nothing has been published concerning the ecology of this species.

Adults, obtained from June, 1966 to April, 1967, were largest and most common from October to November, 1966 (although this may be a reflection of the collection pressure and timing). They were all collected at 20 - 30 m from rocky areas supporting large populations of *Abietinaria rigida* and *A. amphora,* but few other hydroids (with the exception of Lonesome Cove). These areas, often bordered by sandy or muddy bottoms, are usually swept by moderate currents. As mentioned above, *Dendronotus dalli* is able to cling to the hydroids despite these currents.

During a dive off the Victoria Breakwater on August 10, 1966, large numbers of *Dendronotus dalli* egg masses were seen. White, loosely coiled, they were deposited on *Abietinaria rigida,* the rocks, and on other sessile animals such as *Balanus nubilis* and the bryozoan, *Heteropora* sp. During a second dive in late October, 1966, only a few egg masses were seen and in December, 1966 and January, 1968, there were none. One egg mass was collected from Eagle Point on March 27, 1967 and another from Turn Rock on January 21, 1968.

The animals collected in December, 1966, when put in the water tables at the Friday Harbor Laboratories, began to copulate and deposit eggs all during January, 1967. It is difficult to tell whether this was a response to the change in light, temperature, salinity, or substratum; in any case, the gonads were mature when they were collected. A sample from some of these white to cream-colored egg masses contained 4 - 6, 2 - 3, 2 - 3, 3 - 4, 1 - 3, and 6 - 9 eggs per capsule. Hatching, in 4 cases, took 13 - 17, 15 - 18, 17 - 18, 18 - 19 days.

To the human diver's eye, these nudibranchs are visible up to 20 feet against the dark background of the rock and hydroid bed. Presumably fish are also able to see them and, judging from the number of animals with mutilated cerata and rhinophores, probably attack them rather frequently.

Dendronotus dalli is capable of effective, if not prolonged swimming when it is disturbed. So far, only mechanical stimuli such as pinching the cerata has proved effective in eliciting the response. None of the potential predators such as starfish, other carnivorous gastropods, or crabs have shown any effect although, in nature, the reaction to pinching seen in the laboratory may be an effective escape response from a crab. No other methods of defense were obvious, but epidermal secretions are a possibility (Edmunds, 1966; Thompson, 1960b).

Dendronotus rufus O'Donoghue, 1921

(Plate 63, Figure 32; Text figures 4 - 6, 16 - 18)

Dendronotus rufus O'Donoghue, 1921, Trans. Roy. Canad. Inst. **13** (1): 190 - 192; plt. 3, figs. 25 - 27; plt. 4, fig. 48
Dendronotus frondosus (Ascanius, 1774). Odhner, 1936, Mém. Musée Roy. Hist. Nat. Belg., ser. 2, **12** (3): 1105 - 1109

Taxonomic Remarks

O'Donoghue, in describing this species, makes only brief and uncritical reference to the important taxonomic characters. It is little wonder that Odhner (1936, p. 1108) said:

> "*D. rufus* ... has a colour which makes it a probable synonyme [sic] of *D. frondosus,* from which it cannot be separated (according to the description) in external characteristics."

Probably because of his belief that the radula characters in this genus are too variable to be of any use taxonomically, Odhner says nothing about the differences, pointed out by O'Donoghue, between the radula of *Dendronotus rufus* and *D. frondosus.*

O'Donoghue's (1921) largest specimen was only 1.4 cm L while my smallest one was 7.0 cm L and the average was 17 cm L. It is this size discrepancy that made it difficult to determine if the species described below is the same as that described by O'Donoghue. The presence of a red line around the foot and the color of some of his specimens are the most important characters that link my specimens to *Dendronotus rufus.*

The type specimen has apparently been lost (Quayle, pers. comm.; Clarke, pers. comm.; Tebble, pers. comm.), probably during a move of material from the Nanaimo Biological Station to the Canadian National Museum at Ottawa, Canada.

Body Dimensions, Texture, and Apertures

The limaciform body is relatively "heavy," but not as stout in appearance as that of *Dendronotus iris* despite the generally larger size of *D. rufus*. The high, rounded dorsum is confluent with the vertical sides with no sign of a border except the cerata. The animal is laterally compressed, though not markedly so, and tapers to a short, blunt tail.

As noted above, O'Donoghue's specimens were small, the largest being 1.4 cm L × 0.45 cm H × 0.4 cm W and the smallest 0.6 cm L. He subsequently collected a "fairly large" specimen, 1.65 cm L × 0.52 cm H × 0.36 cm W (O'Donoghue, 1922, p. 164). The largest animal of 26 measured in this study was 28.0 cm L × 4.5 cm H × 4.2 cm W while the smallest was 7.0 cm L × 1.5 cm H × 1.0 cm W. Most of the animals were 15.0 - 20.7 (7.0 to 28.0) cm L × 3.0 - 4.0 (1.2 - 4.5) cm H × 2.5 - 3.0 (1.0 to 4.3) cm W.

The anus is on a distinct papilla located about halfway between the first and second right cerata. The top of the papilla is usually magenta like the cerata.

The genital apertures, located about halfway up the side and just anterior to the first ceras on the right, may be quite distinct, depending upon the sexual condition of the animal.

The cardiac prominence is usually indistinct. The body may be smooth or it may have a few small, magenta-tipped, sub-conical papillae widely scattered on the dorsum and the sides. Occasionally, it takes on a wrinkled appearance, particularly if the animal is at all contracted.

Foot

The foot, about 6× longer than wide, is bluntly rounded anteriorly, while the posterior end is bluntly pointed. The edge flares slightly when the animal is crawling on a smooth surface.

The sole of the foot is white. Around the dorsal edge of the foot is a distinct light to dark magenta line made up of small pigment patches. In a few light-colored specimens, this line was not outstanding but it was discernible. In the 2 brick-red animals, this line was dark pink, but because of the body color, it was not so obvious.

Observations in the field and in the laboratory indicate that this species is only partly successful in maintaining its position in a moderately strong current. It also appears unable to grasp the thin stalks of a hydroid, although, considering the size of the animal, this seems reasonable. As yet, nothing is known about the function of the foot in the juvenile stages.

Color

Because color is the important link between O'Donoghue's description and mine, his original account is quoted in its entirety (O'Donoghue, 1921, p. 190):

> "In the living animal, there is a considerable range of colour variation. The general body colour varies from a transparent grey through a semi-transparent pink to a deep brick red. In the grey form, the cerata were of a pale pink colour, in the pink form there was a narrow line of darker, more opaque pink, running around the edge of the foot and up around the head at the anterior end. A similar, but less marked darker line was also present in the red form."

All except 2 specimens that I examined had an opaque, gray-white ground color but, in a few, a liberal sprinkling of very fine magenta dots and some small, magenta-tipped papillae imparted a pinkish hue to the animal (Plate 63, Figure 32). Except in these few extensively pigmented animals, the gray-white color extends for varying distances up the cerata, rhinophores, veil and lip papillae. It merges with a deep magenta pigment which becomes darker and more concentrated towards the distal ends of the above processes. In some animals, the magenta color becomes almost black. In others, it is washed out giving the appendages a distinctly yellow tinge under the magenta. The magenta line around the foot has been mentioned above.

Two specimens were of the "red form" mentioned by O'Donoghue (1921). The ground color is a deep brick-red, lightest on the sides, darker on the dorsum and bases of the appendages, and darkest on the distal portions of the appendages. Scattered over the body and appendages are many small, opaque, yellow to white spots. A few larger, pale cream patches were present on the sides just below the bases of the cerata. Between the cerata, there is an irregularly blotched line of large, opaque white patches extending from the rhinophore to the tip of the tail.

Cerata

The cerata of this species are by far the largest and most dendritic of any of the species of *Dendronotus*. In an animal 14.0 cm L, the tallest cerata were up to 8 cm tall while the widest part of the "ceratal mat" was over 8 cm across. When viewed from above, the body of the animal is almost completely covered by the cerata.

There are 7 - 8 (6 - 9) pairs of cerata placed at slightly decreasing intervals and followed by a single, unpaired ceras in a few animals. The cerata decrease in size also, the last pair being about $\frac{1}{3}$ or less as tall as the first. Between the main cerata are found 4 - 11 "accessory cerata" varying in size from short, simple tufts to arbor-

escent branches nearly as large as the smaller cerata, and pigmented much like the cerata. Although most of them are irregularly placed, there are usually 2 - 4 in a transverse row across the cardiac prominence.

The main branches of the cerata are thick, heavy, and very long. Originating from them are many long and relatively stout secondary branches which in turn divide into long, thin tertiary branches, or which terminate in a bushy tuft of fine filaments. The tertiary branches, fine as they are, often divide to form a smaller bushy tuft.

The pattern of branching is "fan-shaped" (Figure 4a). There are 4 main branches in the first and second pairs of cerata, 3 - 4 in the third, 3 in the fourth, 3 (1 - 3) in the fifth, 2 (1 - 2) in the sixth, and 1 (1 - 2) in the seventh and eighth pairs. The main branches all split off the very short stalk at about the same level. The medial branch (no. 1) and no. 2 are about equal in size, while no. 3 is about $\frac{3}{4}$ as large and no. 4 is about $\frac{1}{2}$ to $\frac{2}{3}$ as large as no. 1. When 3 branches are present, the proportions are about the same but there is only one long medial instead of 2.

Because of the great length of the secondary branches, it is very difficult to determine what to count as main branches and the choice becomes arbitrary especially in the anterior pairs. There is usually a large medial secondary branch arising from the base of main branch no. 1 in the anterior 1 - 4 pairs of cerata. This and a smaller, lateral, secondary branch of main branch no. 4 (or no. 3) of the anterior pair(s) of cerata are particularly difficult to separate from the main branches.

The hepatic diverticula extend into the rhinophores as well as the anterior 4 - 5 pairs of cerata which lie dorsal to the liver. These are visible only after dissection and are limited to the medial 2 - 3 branches of the ceras.

O'Donoghue (1921) described 5 pairs of cerata. The first 3 pairs had 3 simply branched trunks, the fourth pair had 2 simple main trunks, and the members of the fifth pair were simple projections.

Rhinophore and Clavus

The rhinophore, like the cerata, is extensively branched and very tall, reaching as high as the first pair of cerata.

The heavy, firm lateral papilla originates from the base of the stout rhinophore stalk and, despite being at a 30° angle to the stalk, reaches as high as the clavus or even the top of the shorter crown papillae. From the main stalk spring many long secondary branches which may end in bushy tufts or may give rise to slender, tertiary branches that finally end in tufts.

The sub-conical, yellowish to purple-spotted clavus is quite small relative to the size of the animal. There are 19 - 24 alternating shallow-cut leaves as opposed to the 8 - 10 non-alternating leaves mentioned by O'Donoghue (1921). The upper 2 - 4 and lower 4 - 5 leaves are small and equal while on the rest of the clavus the large leaves are about 2× wider than the smaller, and almost completely encircle the clavus.

Radiating from the top of the sheath, like wheel spokes, the 5 crown papillae are long and stout. The branching, usually from the distal half of the papillae, may be restricted to a few relatively simple papillae and tufts or it may be more extensive albeit less so than on the other appendages. The crown papillae are all about equal in length; the longest, the postero-medial, is rarely more than 2× longer than the shortest. Occasionally, the 3 posterior ones are about $1\frac{1}{2}$× longer than the anterior 2.

Head, Lips, and Veil

The 5 pairs of veil papillae are made up of very dendritic, long, thick branches that radiate in an antero-dorsal plane at about 30° from the horizontal. The main branches divide into numerous secondary and tertiary branches just as already described for the cerata and lateral papillae. This type of branching makes it exceedingly difficult to determine what is and what is not a veil papilla. To make it even more difficult, the thick bases of the veil papillae arise immediately adjacent to each other. There is not even a gap in the midline between veil papillae from two sides as there is in the other species.

The medial pair of veil papillae (no. 1) is the largest with no. 3 only slightly shorter. Number 2 pair, originating just ventral and lateral to the base of no. 1, is about $\frac{1}{2}$ to $\frac{1}{4}$ as long as no. 1. Pairs no. 4 and no. 5 are about equal to no. 2, though no. 5 is usually somewhat shorter.

Immediately ventral to the veil papillae are 5 - 10 large, branched papillae that I have called "accessory lip papillae." This name may seem incongruous considering that these papillae are far larger and more branched than the other lip papillae, but they appear to function as veil, rather than lip, papillae; hence the term "accessory."

Posterior to these accessory lip papillae are the true lip papillae. There are 30 or more of these short to long, finger-like projections. A few of the anterior ones may be forked or slightly branched on top. Arranged in vaguely parallel rows coursing fore and aft on either side of the lips, they are longest laterally and shortest near the mouth.

Jaws

The jaws (Figure 16) and buccal mass of *Dendronotus rufus* are remarkably small for so large an animal. From

a sample of 8 buccal masses, the length of the buccal mas was found to be about 1/20 to 1/25 the total length of the body.

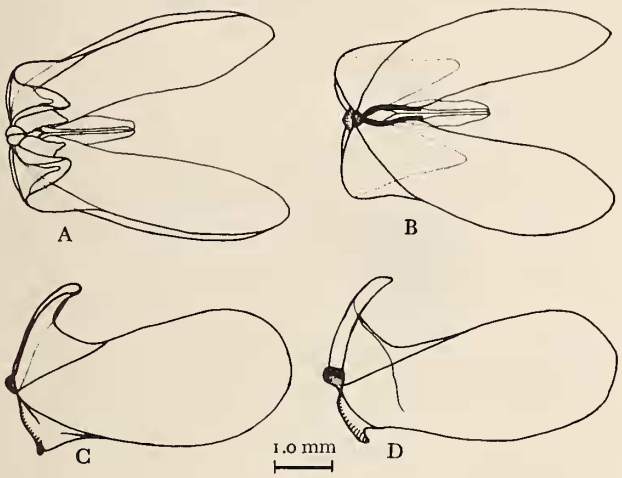

Figure 16

Dendronotus rufus jaw
A. Dorsal view B. Ventral view C. Inside lateral view
D. Outside lateral view

The light yellow jaws are relatively thin and delicate. The body is a moderately convex, mytiloid form, slightly wider in the posterior third and about 2.2× longer than wide. The dorsal process, about 0.45× as long as the body and inclined at a 70° angle with its long axis, is joined to the body by a strongly convex expansion throughout half or more of its length. The distal portion of this broad, heavy dorsal process is curved downward and the dorsal groove is deeper and wider than in any other species.

The masticatory process, at a 75° angle with the long axis of the body, is joined to the body by a strong, shallowly concave expansion and bears numerous rows of narrow, low denticles.

Radula

O'Donoghue (1921) described a radula formula of 32 - 35 (6 - 8 · 1 · 6 - 8): the laterals had 3 - 6 stout denticles while the medians bore 10 large sharp denticles. In contradistinction to this, in the 9 radulae that I examined, the formula was 33 - 35 (10 - 16 · 1 · 10 - 16). The laterals have a variable number of short denticles, and the medians bear many short, blunt denticles (Figure 17). If the animals O'Donoghue describes are juveniles of this species, then it seems that there must be a marked change in the radula characteristics during an individual's life; it may be these transition stages which cause the confusion about which Odhner (1926) writes.

The cusp of the median tooth, rounded or bluntly pointed at the apex and very weakly bulged on the sides, is usually about 1.5 - 1.7× as wide as long, but in a few posterior teeth the ratio may increase to 2× (Figure 6 for measurements). The denticulation of the cusp varies considerably. There are commonly 16 - 22 (6 - 28) small, blunt, more or less regularly spaced, denticles diminishing in size towards the apex and sometimes disappearing altogether. The indentations of the proximal denticles continue on the dorsal surface of the cusp as fine, shallow furrows, giving the tooth a delicately corrugated appearance. In a few specimens, there is only a fine serrulation along the edge while in a few others, the older teeth may be quite jagged where pieces have apparently been broken off. On any particular radula, the number of denticles on the median tooth generally increases from the oldest teeth to the newest.

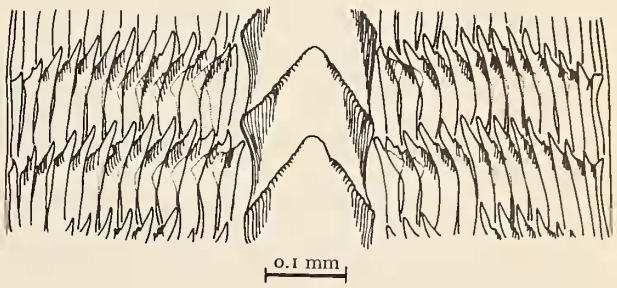

Figure 17

Dendronotus rufus radula
Rows 21 and 22 in a radula with 36 rows of teeth

Most of the tall, stout lateral teeth bear a strong, bluntly-pointed, straight cusp markedly inclined (20 - 30°) toward the midline. The inner few teeth have a distinct protuberance on the lateral border at the base of the cusp. In a transverse row, the cusp increases in size from a short, often insignificant quantity in teeth no. 1 and no. 2 to a maximum length in teeth no. 6 to 8 and then decreases again, often disappearing in the outermost 1 or 2 teeth.

The denticulation of the lateral teeth is quite variable. Generally, the short, sharp denticles do not project very far above the lateral border of the cusp and then continue down the face of the base as relatively deep, distinct furrows. There is a vague tendency for the number of denticles per tooth to increase from anterior to posterior rows while within a row it is greatest at teeth nos. 4 - 7, and decreases on either side. The following list of denticle

numbers per lateral tooth is compiled from counts made on 6 rows at various points along the radula for 9 radulae.

The numbers in parentheses represent extremes while those outside represent 70% of the teeth.

Lateral Tooth (numbered from medial to lateral)	Number of Denticles
1	none 50% of time; 1 - 4 otherwise
2	0 - 3 (0 - 5)
3	0 - 3 (0 - 6)
4	2 - 4 (0 - 6)
5	2 - 5 (0 - 7)
6	1 - 6 (0 - 8)
7	3 - 5 (0 - 9)
8	0 - 6 (0 - 9)
9	0 - 3 (0 - 8)
10	0 - 2 (0 - 7)
11	0 - 1 (0 - 6)
12	0 - 1 (0 - 2)
13	0
14	0
15	0

Reproductive System

The reproductive system (Figure 18) may be concisely described as "long."

The large, white hermaphrodite gland of sexually mature animals appears gray in immature animals because of the small black spots on the lobules. The hermaphrodite duct expands suddenly to form a long, narrow ampulla, exceeded in relative length only by that of *Dendronotus iris*. The ampulla narrows rapidly to form the short spermoviduct that bifurcates to form a very short, transparent, rugose oviduct and an equally short proximal portion of the vas deferens.

The vas deferens expands to form the prostate, a relatively enormous sphere concentric with the vas deferens and comprised of many small to large irregularly shaped alveoli. From this large prostate arises a very long, narrow, extremely convoluted and coiled distal portion of the vas deferens. It tapers very gently throughout its whole length to become a thin tube. As such, it enters the base of the penis to form the long, convoluted ejaculatory duct. The long slender penis, coiled and folded back on itself in the preputium, is tapered to a slightly bulbous tip. The male portion of the *Dendronotus rufus* genital apparatus is most distinctive: the prostate is larger, the vas deferens is longer and more convoluted, and the penis is relatively longer and thinner than in any other species in the genus.

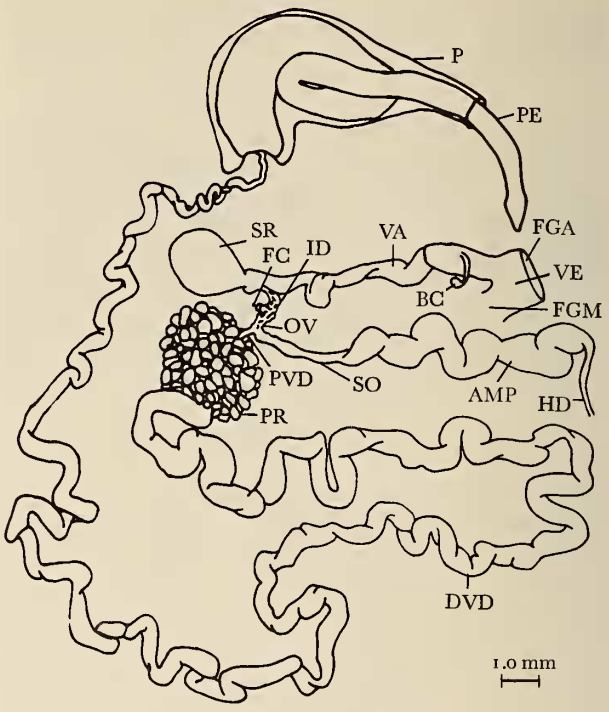

Figure 18

Reproductive system of *Dendronotus rufus* (exploded view)
AMP = ampulla BC = bursa copulatrix
DVD = distal vas deferens FC = (to) fertilization chamber
FGA = female genital aperture FGM = (to) female gland mass
HD = hermaphrodite duct ID = insemination duct
OV = oviduct P = preputium PE = penis
PR = prostate PVD = proximal vas deferens
SO = spermoviduct SR = seminal receptacle VA = vagina
VE = vestibule

The long but narrow and tortuous vagina terminates proximally in a large, nearly sessile, ovoid seminal receptacle. The bursa copulatrix, not much wider than its long stalk, is located near the opening of the vagina into the vestibule. A very short insemination duct is applied to the outer surface of the vagina for a short distance before joining the oviduct.

Geographical Distribution

O'Donoghue (1921, 1922, 1924) collected *Dendronotus rufus* at Departure Bay, Nanoose Bay, Breadwater Island, and Thetis Island, all in the Strait of Georgia, B. C. The depth range was 20 - 40m.

The specimens collected for this study were obtained at Alki Point, Seattle (23 animals) from 15 - 17 m; Departure Bay, Nanaimo (1 animal) from 20 m; Brown Island in Friday Harbor (1 animal) from 7 m; and the floats at Jensen's Boat Yard, Friday Harbor (2 animals).

Ecology

Juveniles of this species have not been seen, but adults were found from November, 1966 to March, 1967 and again from January to March, 1968. *Dendronotus rufus* seems to prefer areas of slight to moderate current action possibly because of the apparent inability to hold on in swift currents. The substratum has usually been rock surrounded on all sides by sand or mud or both.

Examination of the fecal pellets plus observations in the field and laboratory indicate that scyphistomae, when present, form part of the diet of the Alki Point population of *Dendronotus rufus*. Nothing else was found in their guts except for a few amphipods that occurred on the scyphistomae. The fecal pellets of the animals collected at areas other than Alki Point contained no nematocysts or anything else recognizable.

During late January, 1967, nudibranchs collected two months previously began depositing egg masses in the aquarium. Shortly after, on February 2, 7 egg masses were seen at Alki Point on the rocks and pipe. The animals collected then plus the previous group (16 in all) laid about 60 nidosomes up to the end of March when they all died. During January and February, 1968, about 100 copulating pairs were seen at Alki Point and 175 - 200 egg masses were deposited during February. By March 20, 1968, all the animals plus the egg masses were gone. In the field as well as the laboratory, the white to cream colored egg string was deposited in a regular though loose spiral. The number of eggs per capsule varied from 4 - 5 to 17 - 27, with an average of 13 - 17. The length of time from oviposition to hatching of the veligers varied from 13 - 20 days with most hatching in 15 - 18 days.

Only because of its large size is *Dendronotus rufus* easy for a diver to see in the field. The dark cover provided by the cerata helps the animal to blend in with the background, at least those upon which it has been seen. *Dendronotus rufus* appears to be a very poor swimmer responding quite slowly to strong mechanical stimulation. The species has a possible defense mechanism that the rest of the *Dendronotus* species lack: a thick, extremely sticky mucus. This mucus makes the animal slippery to hold, but, more important, it would probably "gum up" the mouth or claws of a predator due to its adhesive qualities. Predators may also find it repulsive to the taste. Whatever the particular defense mechanism, it must be effective for I have seen no mutilated specimens or evidence of attack as was so often seen in other species.

Dendronotus gracilis Baba, 1949

Dendronotus gracilis Baba, 1949, Opisthobr. Sagami Bay, pp. 87 - 88, 167; fig. 109; plt. 35

Taxonomic Remarks

To describe the internal and external structure and ecology of *Dendronotus gracilis,* I have used the description, text figures, and plates given by Baba (1949) supplemented by information from Dr. Michael Miller. Baba's data have been rearranged to suit the format I have used in this paper.

The radula of *Dendronotus gracilis* is not very different from that of *D. albus* or the new species, although that of the new species usually has more denticles on the lateral teeth. The number of cerata (4 pairs) and their branching pattern (very few secondary branches) in *D. gracilis* is markedly different from that of *D. albus* (5 - 7 pairs of cerata with considerable secondary and tertiary branching). Also the coloration of *D. gracilis* is distinctly different from that of any other species of *Dendronotus.* Neither the reproductive system nor any aspects of ecology are mentioned by Baba (1949).

Body Dimensions, Texture, and Apertures

The largest specimen of this limaciform, relatively "delicate" species was 2.5 cm L (Baba, 1949). Miller (pers. comm.) reports that his largest specimen is 0.6 cm L. Width and height are not given in either case.

The anus is on the right side between cerata no. 1 and no. 2. Below and just anterior to the first right ceras lies the genital aperture. The cardiac prominence is not mentioned. According to Baba (1949), the body is smooth, but Miller (pers. comm.) says the body is covered with small conical tubercles.

Foot

There is no mention of the foot by Baba (1949). The figure (Baba, *op. cit.,* plt. 35) shows the dorsal aspect of the animal so no information regarding the foot can be obtained from it.

Color

The body color is bluish-white and the cerata, crown and veil papillae are opaque white. The clavus of the rhino-

phore is dark yellow (Baba, 1949) or opaque white (Miller, pers. comm.). This color pattern is somewhat akin to that of *Dendronotus albus,* but the rest of the "coloration of [*D. gracilis*] is unmistakable" (Baba, *op. cit.*, p. 167).

About 15 "yellow ocelli, each with an orange spot in the centre, are irregularly scattered on the back [dorsum]" (Baba, *loc. cit.*). The color plate also shows what may be 4 patches of white pigment in a mid-dorsal medial line extending from the posterior pair of cerata to the tip of the tail (these may also be the 2 "accessory cerata" mentioned below; see Cerata). Miller (pers. comm.) noted 5 longitudinal rows of yellow spots: 1 mid-dorsal, 2 dorso-lateral, and 2 lateral.

Cerata

Baba (1949) mentioned 4 pairs of short cerata while Miller (pers. comm.) found 5 pairs on the 0.6 cm animal. These divide into 2 or 3 main branches in what appears to be a "rosette" pattern (Figure 4b). There are fewer secondary branches than in any other species of *Dendronotus* and tertiary branches appear to be lacking completely. Posterior to the last pair of cerata are 2 "accessory cerata," the size and branching pattern of which is not described.

Rhinophore and Clavus

There is neither a lateral papilla nor a posterior crest (such as *Dendronotus iris* has) on the round rhinophore stalk. The clavus is perfoliate with 8 - 17 leaves (Baba, 1949, text fig. 109b; Miller, pers. comm.). There are 4 - 6 simple or branched, approximately equal, but short crown papillae around the relatively large clavus.

Head, Lips, and Veil

Baba (1949, p. 167) described 4 relatively simple, approximately equal veil papillae. However, the diagram (text figure 109a) shows a third pair of short, simple papillae between the medial (no. 1) and lateral (no. 3?) veil papillae. No lip papillae are mentioned or diagrammed.

Jaws

The jaw is about 2.5 mm L or about a tenth the length of the animal. The long axis of the dorsal process is at nearly right angles to the long axis of the body of the jaw (Baba, 1949, text fig. 109d). This is a greater angle than seen in any of the other species of *Dendronotus* and may be one of the more useful taxonomic characters of this species.

The masticatory process of the jaw sports about 40 hook-shaped denticles along the masticatory border.

Radula

The radula formula is 41 (8 · 1 · 8) in the one specimen Baba (1949) examined. On each side of the median tooth cusp there are 17 - 20 relatively small denticles decreasing in size towards the apex. The cusp is quite low, being about $2\frac{1}{2}\times$ as wide as high (Baba, *op. cit.*, fig. 109f).

Of the 8 lateral teeth, the medial 6 have cusps and denticles while the outer 2 have neither. The cusp of the no. 1 lateral tooth is about equal in size to the 4 denticles of that tooth. In teeth nos. 2 - 4 the cusp increases in size and then decreases in nos. 5 - 6. On teeth nos. 2 - 6, there are 7 - 9 denticles which are largest on no. 2 and decrease progressively to become mere serrulations on no. 6.

Reproductive System

No mention is made of the reproductive organs by Baba (1949). A detailed description of the system would be useful in more securely identifying the status of this species within the genus.

Geographical Distribution

Baba's one specimen was collected in August, 1939, from 160 m at Amadaiba, Sagami Bay, Japan. Miller (pers. comm.), dredging from 9 - 24 m in New Zealand waters, collected 2 specimens on hydroids growing on *Glycimeris* valves.

Dendronotus subramosus MacFarland, 1966

(Plate 64, Figure 33; Text figures 3, 4, 6, 19 - 21)

Dendronotus subramosus MacFarland, 1966, Mem. Calif. Acad. Sci. 6: 265 - 270; plt. 40, fig. 3; plt. 46, figs. 5 - 8; plt. 47, figs. 3 - 7; plt. 49, figs. 1 - 3; plt. 50, fig. 2 plt. 52, figs. 1 - 2

Taxonomic Remarks

Except for the original description, no information concerning *Dendronotus subramosus* has been published. Marcus (1961, p. 34) includes, under *D. frondosus,* animals which " . . . are translucent grey with two brown stripes on either side between the insertions of the cerata . . .." but these are probably *D. subramosus.* Ecolog-

ical as well as morphological data lead me to consider *D. subramosus* a valid species, distinct from *D. frondosus*.

Body Dimensions, Texture, and Apertures

The limaciform, moderately "heavy" body, is laterally compressed. The rounded dorsum merges into the vertical sides with no distinct dorso-lateral boundary save the cerata (Figure 3). The largest animal that I have found was 6.5 cm L × 1.8 cm H × 0.9 cm W while that of MacFarland (1966) was 4.0 cm L × 0.8 cm H × 0.55 cm W. The mode was about 2.8 - 3.0 cm L (0.3 - 3.9 cm) while the mean length, 2.4 cm, agrees well with that of MacFarland's 2.5 cm. Some others measured were: 0.9 cm L × 0.15 cm H × 0.2 cm W; 2.4 cm L × 0.4 cm H × 0.35 cm W; 2.3 cm L × 0.5 cm H × 0.35 cm W.

The anus is usually inconspicuously located about halfway along the outermost dark brown line between no. 1 and no. 2 right cerata (see Color, below). The anal papilla, if present, may be capped by yellow pigment.

The genital openings are from $\frac{1}{2}$ to $\frac{2}{3}$ the way up the right side, just anterior to the base of the first ceras. They are relatively inconspicuous except that the tip of the preputium often has a ring of pale yellow pigment around it.

The cardiac prominence is usually quite large, but in a few animals it was indistinct. To some degree, the size can be altered in the individual.

The body and appendages may be smooth, but more often they are covered with relatively small, closely-set, sub-conical to conical papillae. These papillae range in size up to 3 mm, the largest ones usually situated on the dorsum, especially the cardiac prominence, while the smaller ones are on the sides and the appendages. Often patches of lemon-yellow or white pigment adorn the papillae.

Foot

The long, narrow foot is bluntly rounded anteriorly and comes to a short, blunt point posteriorly. The sole of the foot is a translucent pinkish-white. When crawling, the edge of the foot is often flared laterally, especially in the posterior half. In a specimen 2.3 cm long, the foot was 2.0 cm L × 0.25 cm W while, in a 4.0 cm specimen, MacFarland (1966) found the foot to be 3.7 cm L × 0.35 cm W.

The foot, the edges of which are able to fold together very easily, is well adapted for clinging to the hydroid, *Aglaophenia struthionides,* upon which *Dendronotus subramosus* is usually found. It is only with much difficulty that the animal can be shaken from its perch; a most useful attribute considering that it often occurs in areas of considerable current action.

Color

The ground color varies from white (13 specimens) to dark brown (3 specimens) with a few being pale yellow, deeper yellow or bright orange (9 specimens). Most are reddish-brown (41 of 66) (Plate 64, Figure 33). A liberal sprinkling of pale lemon-yellow or orange spots is densest on the tips of the appendages, less so on the dorsum and sparsest on the sides. There are also variable numbers and combinations of tiny brown, red-brown, gold, green, and white spots intermingled with the former.

A distinct pattern of 4 light to dark brown, longitudinal lines is usually seen in the intervals between the dorsal appendages. The outermost line on each side connects the lateral base of the rhinophore stalk with the lateral base of each successive pair of cerata and carries on to the tip of the tail. Likewise, the inner line on each side connects the medial base of the rhinophore stalk to the medial base of each successive ceras and again is extended towards the tail where all 4 lines merge. These lines, particularly the posterior or medial ones, or both, may be found wanting in lighter colored animals. The areas between the lateral and medial dark bands are usually devoid of brown pigment but often are liberally covered with yellow or white spots.

Cerata

There are usually 5 (3 - 6) pairs of stout, upright cerata spaced at posteriorly decreasing intervals along the dorso-lateral borders of the body with an occasional single ceras at the posterior end (Figure 3). The size and degree of branching of the cerata also decreases from anterior to posterior.

The thick stalks subdivide about halfway up the total height of the cerata in a "rosette" pattern (Figure 4b). Determining the number of main branches may be difficult, but there are usually 3 (2 - 4) main branches in each ceras of the first pair, 2 (2 - 4) in the second pair, 2 (1 - 4) in the third pair, 2 (1 - 4) in the fourth pair, and 1 (1 - 2) in the fifth pair. The postero-medial branches are usually the longest and most branched. The lateral branch, found arising from the base of the ceras in all the other species is missing in this animal. There are relatively few of the stout secondary branches and

even fewer of the very short, simple tertiary branches making the ceras less delicately and complexly branched than is common in the genus.

Only the first pair of cerata, as well as the rhinophores, receives hepatic diverticula which arise from the anterior lobes of the liver; there are no diverticula from the posterior lobe.

Rhinophore and Clavus

The rhinophore (Figure 3), stout, erect, and inclined slightly forward when the animal is crawling, completely lacks a lateral papilla.

The perfoliate, bluntly conical clavus carries 9 - 14 (3 - 14) leaves (8 according to MacFarland, 1966). The number appears to be related to size, the small animals (0.3 - 0.9 cm L) having 3 - 6 leaves and the larger ones (3.7 - 6.5 cm L) having 12 - 14 leaves. These leaves are relatively shallow (narrow in breadth) and show little alternation in size although they do become smaller near the top. The coloration of the clavus matches that of the rest of the body.

The campanulate rhinophore sheath has 5 (3 - 7) short, blunt crown papillae. About equal in size, the papillae are not much taller than the extended clavus; the posteromedial is the longest by about $1\frac{1}{2}\times$. A few small branches may be found on the longer crown papillae, but the rest are simple.

Head, Lips, and Veil

On a very distinct horseshoe-shaped veil, there are usually 2 pairs of veil papillae (Figure 3). There may occasionally be a third pair (MacFarland, 1966) or, more commonly, an extra papilla on one side or the other.

The medial pair (no. 1) of veil papillae is the longest and normally points straight ahead when the animal is crawling. About $\frac{1}{2}$ to $\frac{2}{3}$ as long as the medial pair, the lateral pair (no. 2) is usually directed at right angles from the body. If a third pair (or one of the pair) is present, it usually is a mere tubercle positioned laterally to no. 2. Pairs no. 1 and no. 2 are both stout, with only a few short, blunt branches being given off, usually from the distal half of the papillae.

MacFarland (1966) neither mentions nor figures any lip papillae, but I found 2 (1 - 4) in about 50% of the animals examined. They are short and simple, arising at the posterior end of the lips.

Jaws

The jaws (Figure 19) are a striking reddish-brown, darkest on the hinge and middle of the body, and becoming lighter around the edges of the body and on the dorsal process.

The main body of the mandible, thin, mytiloid, and ovate in form, is slightly more than half as wide as long.

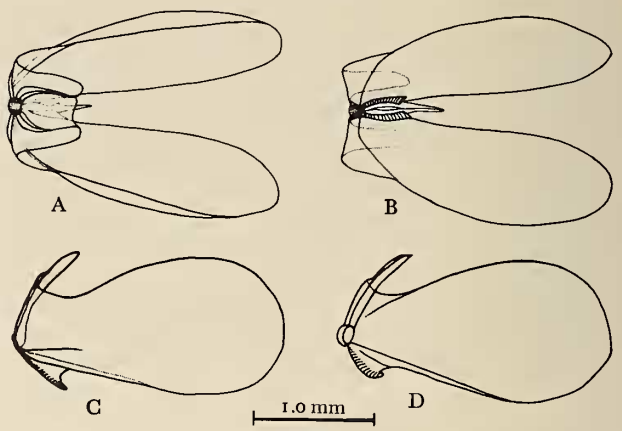

Figure 19

Dendronotus subramosus jaw
A. Dorsal view B. Ventral view C. Inside lateral view
D. Outside lateral view

The dorsal process, curving backward at about 65° from the longitudinal axis of the body, is about $\frac{1}{3}$ as long as the body, shallowly grooved dorsally, and rounded at the tip. The triangular expansion, joining the proximal half of the dorsal process to the body, bulges outward only moderately.

According to MacFarland (1966), the short, curved masticatory margin is armed with about 120 closely set, transverse, smooth, crescentic plates, narrowest at the hinge and largest at the distal end. The masticatory process is joined to the body by a thin, inward-bulging plate.

Radula

The radula formula is 59 - 72 (5 - 7 · 1 · 5 - 7) according to MacFarland; I found it to be 54 - 62 (2 - 5 · 1 · 2 - 5) in the 5 specimens I examined (Figure 20). The medial tooth has a small cusp, the width : length ratio being about 2 : 1 (Figure 6 for measurements). Seven to 10 (2 - 12) long, heavy denticles, becoming smaller towards the apex, adorn each side of the cusp. The oldest teeth often have only 2 denticles, only slightly smaller than the main cusp and set off from it. Most of the rest are like those shown in Figure 20, although, in the youngest medial teeth, the cusp may be crescent-shaped.

The lateral teeth are flat, often irregularly shaped plates. At the anterior end of the radula, there is usually only 1 tooth on either side, but this number increases to about 3 (2 - 4) a third of the way along and by the half to two-thirds point, the full complement of 5 (4 - 7) teeth is usually present. The pointed, spike-like cusp is

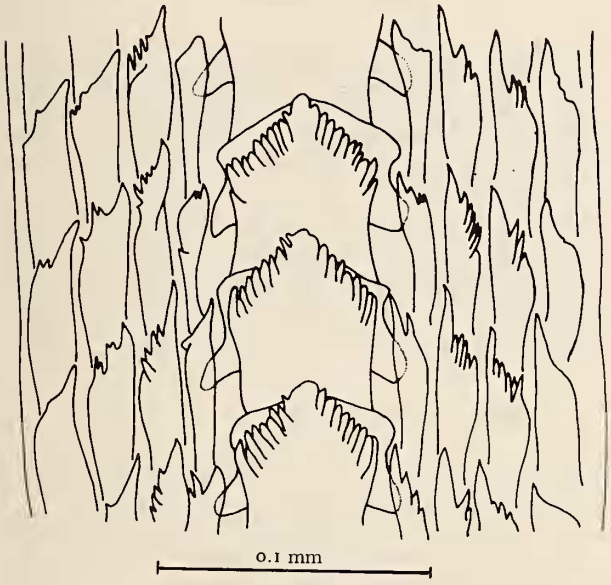

Figure 20

Dendronotus subramosus radula
Rows 34 and 35 in a radula with 53 rows of teeth

variable in length, being short on no. 1, longest on no. 2 and no. 3, shortest on no. 4, and missing on nos. 5 to 7. Teeth nos. 5 - 6, when present, are usually narrow, lacking both cusps and denticles, while no. 7 is a mere rudiment. The denticles, moderately sharp and long, are usually variable in shape and orientation. Tooth no. 1 has 3 (2 - 6) denticles about equal to the cusp in size; no. 2 has 5 - 6 (2 - 8) long denticles; no. 3 has 3 - 4 (2 - 8) shorter denticles; no. 4 has 2 (0 - 4) short denticles; and nos. 5 - 7 have none.

Reproductive System

The hermaphrodite duct joins the white to light pink hermaphrodite gland to the short, thick, crescentic ampulla (Figure 21). The comparatively long spermoviduct arising from the ampulla bifurcates to form a short proximal portion of the vas deferens and a somewhat longer thin-walled oviduct, contrary to what MacFarland (1966) figures.

The prostate, composed of 6 - 7 alveoli (10 - 12 according to MacFarland) forms a single circle around the duct. The convoluted, fairly short, distal portion of the vas deferens tapers considerably from a wide, thick-walled duct near the prostate to a very narrow tube where it enters the base of the penis. The long, thin penis, extensively coiled in the thin-walled preputium, is tapered throughout its whole length.

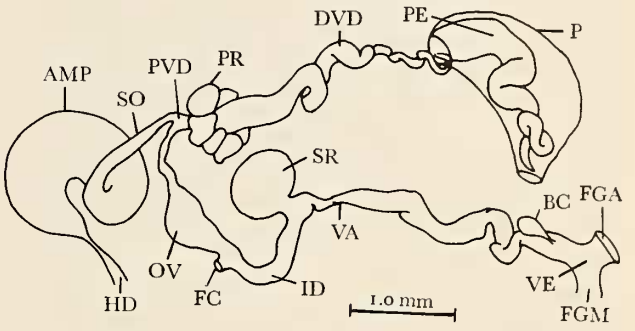

Figure 21

Reproductive system of *Dendronotus subramosus* (exploded view)
AMP = ampulla BC = bursa copulatrix
DVD = distal vas deferens FC = (to) fertilization chamber
FGA = female genital aperture FGM = (to) female gland mass
HD = hermaphrodite duct ID = insemination duct
OV = oviduct P = preputium PE = penis
PR = prostate PVD = proximal vas deferens
SO = spermoviduct SR = seminal receptacle VA =vagina
VE = vestibule

The vagina is slender and somewhat convoluted before it gives rise to the short, stalked, spherical seminal receptacle. This in turn gives rise to a short, thick insemination duct. The small, sac-like bursa copulatrix is located near the opening of the vagina into the vestibule.

Geographical Distribution

In California, MacFarland (1966) reports *Dendronotus subramosus* in the intertidal from Humboldt Bay to Newport Bay and especially in Monterey Bay. Lance (pers. comm.) has collected the species in the *Macrocystis* sp. canopy at 18 m just south of South Island, Islas Los Coronados, Mexico. Locally, it has been collected from San Juan Channel, Edwards Reef, Lonesome Cove, Low Island, and Peavine Pass, all sub-tidally.

Ecology

MacFarland (1966) found *Dendronotus subramosus* most commonly in tide pools during the summer, but it

was present all year long. Locally, I found it most commonly from June to November, but this may reflect the timing of collecting trips.

I collected *Dendronotus subramosus* in 15 - 30 m of water (except for 5 specimens dredged from 120 m in San Juan Channel), but I have not seen them intertidally despite many collecting trips. All the collection sites are swept by fast currents, up to 4 knots or more. The bottom is generally composed of gravel, shell, and sand, over which are scattered many small to large stones. This type of bottom normally supports an extensive hydroid fauna including *Aglaophenia struthionides* upon which *D. subramosus* are found. In the laboratory, they showed a preference for *Aglaophenia* over any other substratum about 90% of the time. The food of this species consists of whole hydranths of *A. struthionides* as well as sections of the coenosarc that are drawn through holes rasped or chewed in the perisarc.

Animals with a mature hermaphrodite gland were found from October to November, 1966 and one in February, 1967. During this period of time (October to November) about 10 egg masses were deposited in the aquaria. At the same, in the field, many egg masses were seen on the top third of the *Aglaophenia* fronds. During June and July, 1967, about 150 egg masses were seen at Low Island and Edwards Reef, again on *Aglaophenia.* This placement of the egg masses seems disadvantageous in that they are probably visible to any hungry fish. On the other hand, it exposes the egg mass to the current, thus keeping it relatively clean and facilitating the dispersal of the planktonic veligers. Also, those smaller, benthic predators that might otherwise eat the eggs probably do not detect them when the eggs are high off the bottom.

The white to pink egg masses are laid in a loosely coiled string which itself is arranged in a loosely spiralled clump and attached to the substratum by a capsule-free mucous sheet. In the 4 cases timed, the veligers hatched 15 - 18 days after oviposition.

Dendronotus subramosus on *Aglaophenia* is most cryptic and it is only with careful searching that one is able to find it amongst the branches of the hydroid, particularly while diving. Only the very light colored ones are visible against the dark brown of the hydroid. The nudibranch is able to swim clumsily when disturbed. It has no other obvious means of defense, so perhaps its cryptic coloration is its main means of survival.

Dendronotus albus MacFarland, 1966

(Plate 64, Figure 34; Text figures 2, 4 - 6, 22 - 24)

Dendronotus albus MacFarland, 1966, Mem. Calif. Acad. Sci. 6: 275 - 279; plt. 40, fig. 1; plt. 46, figs. 1 - 4; plt. 47, figs. 8 - 11; plt. 48, figs. 7 - 8; plt. 49, fig. 5; plt. 50, fig. 4; plt. 51, figs. 6 - 7

Taxonomic Remarks

The description of this species is based on the extensive descriptions of each of 81 animals collected between September 14, 1966 and January 2, 1967 at various points around San Juan Island. About 100 more animals were examined to see how much, if any, variation there was from the first group.

The reader is referred to the section on Taxonomic Remarks under the new species of *Dendronotus* for a discussion of the difficulty of separating it from *D. albus.* Also included is a discussion of why I have considered the two species distinct.

Body Dimensions, Texture, and Apertures

The long, slender, moderately compressed body is quite "delicate" as might be expected in an animal this small. The rounded dorsum tapers posteriorly to a short, narrow, sharp-pointed tail, and merges laterally with the nearly vertical sides with no hint of a border save the cerata (Figure 2).

The largest animal was 4.0 cm L, and the shortest was 0.4 cm L. MacFarland (1966) reports a maximum size of 3.0 cm L × 0.5 cm H × 0.3 cm W. Most of the animals were between 1.5 and 2.5 cm L with an average of 1.9 cm L. Some representative measurements are: 1.4 cm L × 0.4 cm H × 0.25 cm W; 1.8 cm L × 0.3 cm H × 0.35 cm W; 2.3 cm L × 0.35 cm H × 0.3 cm W; 2.9 cm L × 0.3 cm H × 0.25 cm W. The adult size is thus much smaller than that of the new species of *Dendronotus.*

The anus is borne on a small papilla located halfway between no. 1 and no. 2 pairs of cerata on the right side. Often, the top or the sides of the papilla, or both, are encrusted with an opaque white pigment.

The genital orifices are situated about $\frac{2}{3}$ of the way up the body just anterior to the base of the first right ceras. The distal end of the preputium often protrudes and bears a white pigment spot.

The cardiac prominence may be markedly elevated and it can vary in an individual. Most of the body surface

is smooth, but about 50% of the animals have few to many small, bluntly conical papillae on the dorsum. They are largest and most common on the cardiac prominence. The yellow pigment which normally appears on these papillae forms what looks like a small peg passing into the dermis.

Foot

The long, narrow foot, about 8 - 10× longer than wide, is bluntly rounded anteriorly and tapers fairly sharply in the posterior quarter to a point. In an animal 2.65 cm L, the foot was 2.4 cm L × 0.3 cm W. When the animal is crawling, the foot flares laterally, especially in the posterior third. The sole of the foot is translucent white.

Dendronotus albus can cling so tightly to a hydroid that it is extremely difficult to shake it loose and one must resort to peeling the nudibranch away from the stalk of the hydroid. This clasping ability enables the nudibranch to remain on the hydroid, *Thuiaria argentea,* in the face of some very strong currents.

Color

The translucent body is usually white although a few pale cream or pink-brown specimens were seen (Plate 64, Figure 34). The color of these latter is due to a dense sprinkling of tiny, opaque, white, yellow, or pink-brown spots over the dorsum and appendages. One animal was a medium red-brown color, palest on the sides and darkest on the dorsum and cerata. The internal organs show through as a red-brown or white mass, depending on the animal's sexual maturity.

The pattern of encrusting, opaque, dead-white pigment consists of solid white lines or broken patches in varying amounts on the postero-medial (or occasionally antero-medial) face of the cerata's main branches; the posterior face of the rhinophore stalk and the posterior crown papillae; and the dorsal surface of the veil papillae. A dorso-medial white line begins between the second and fifth pairs of cerata and extends to the tip of the tail. Anteriorly, it may be broken up into irregular patches.

The cerata are striking in many specimens. The brown hepatic diverticula become a very dark, rich brown about $\frac{1}{4}$ to $\frac{1}{2}$-way up the branch. From about $\frac{1}{2}$ to $\frac{2}{3}$ of the way up, this brown merges with a very beautiful metallic orange or copper pigment, and this in turn merges with the opaque, dead-white pigment near the tip. In a few specimens, the orange or copper pigment was missing, being replaced by the white while a few others lacked both pigments and the brown of the diverticula continued to the top. This elegant pigmentation normally only occurs on those branches containing hepatic diverticula, but all the other main branches do have the white pigment on the tips.

Cerata

There are 5 - 7 (4 - 8) pairs of tall, delicate, moderately branched cerata arranged at posteriorly decreasing intervals on either side of the dorsum (Figure 2). The height of the cerata also decreases posteriorly and the last pair is often less than a quarter as tall as the first pair. In almost half of the animals, there are one or two short, simple, unpaired posterior papillae.

The main branches are long and slender with a few relatively long secondary branches. In contrast to the new species of *Dendronotus* there are many small, almost transparent tertiary patches giving the cerata a "bushy" appearance.

The branching pattern is "fan-shaped" (Figure 4a) with 3 main branches in the first and second pair of cerata, 2 - 3 in the third pair, 2 (1 - 3) in the fourth pair, 1 - 2 in the fifth pair, and one in pairs 6 to 8. In those pairs with 3 branches, the lateral branch, from $\frac{1}{2}$ to $\frac{2}{3}$ as long as the medial, arises from the base of the ceras. The main stalk then branches a short distance above this into 2 almost equal branches. When there are only 2 main branches, the medial is from 2 - 4× longer than the lateral which again arises from the base of the ceras. This lateral branch decreases in size from anterior to posterior and, in the last two pairs of cerata, it is usually missing.

The hepatic diverticula extend into the 2 medial branches (trifid cerata) or the single medial branch (bifid cerata) in the first to fourth (1 - 6) pairs of cerata as well as the rhinophore stalk and posterior crown papillae. The anterior lobes of the liver give rise to the diverticula of the first pair of cerata and the rhinophore while the posterior lobe gives rise to the rest of the diverticula.

Rhinophore and Clavus

The erect, delicate rhinophore bears few branched processes, much like the new species of *Dendronotus.*

The lateral papilla, varying in length from a mere bump to a relatively long, slender papilla, is usually unbranched or, at most, bears a few small, simple papillae. It arises about $\frac{1}{3}$ to halfway up the rhinophore stalk.

The conical, perfoliate clavus bears 13 - 17 (12 - 22) deeply-cut, alternating leaves (12 - 14 according to MacFarland, 1966). These are usually peppered with pinkish spots that impart a distinctly tan color to the clavus.

Often, the distal half of the clavus is bent forward 90 to 120° from the vertical.

The slender, unbranched crown papillae are directed obliquely upward, but are so tall that they tend to droop outward. The anterior 3 are shortest and about equal in length. The postero-medial one is about 3 (2 - 4)× as long as the anterior ones and often stands taller than the rhinophore stalk. The postero-lateral papilla is often nearly as long as the postero-medial and usually at least 2× longer than the anterior papillae.

Head, Lips, and Veil

These structures are remarkably similar in size and location to those in the new species of *Dendronotus*. The 3 pairs of long, slender veil papillae are usually simple (Figure 2). Sometimes they have a few short, simple secondary papillae and, only rarely, very few tertiary branches. The medial pair (no. 1), directed forward and slightly upward, is the longest. The middle pair (no. 2) is about $\frac{1}{2}$ to $\frac{1}{5}$ as long as the medial pair, originates ventro-lateral to the base of no. 1 and is directed ventro-medially, in a hook-like fashion, toward the mouth. About $\frac{3}{4}$ of the length of no. 1, the lateral pair is often split into 2 rami with the lateral ramus about $\frac{1}{4}$ to $\frac{3}{4}$ as long as the medial ramus. Both rami are directed upward and laterally at 70 - 90° from the long axis of the body.

There are 2 - 4 (0 - 8) long, thin, blunt, unbranched lip papillae located on the posterior border of the plicated lips and lateral to the mouth. Being very sensitive, these papillae retract rapidly if touched, thus possibly accounting for the wide range in numbers observed.

Jaws

The jaw (Figure 22), very small and fragile, is nevertheless relatively large for an animal of this size. In a preserved specimen 1.2 cm L (1.5 cm L when alive), the jaw was 0.22 cm L × 0.19 cm W × 0.15 cm H (Figure 5 for measurements) about a seventh as long as the animal. The body of the jaw is a horn yellow while the hinge area, masticatory process, and most of the dorsal process are a darker brown, gradually fading to horn yellow near the body. The right and left halves of the jaw diverge posteriorly more than in any other species of the genus; this is even more pronounced when all the musculature is removed.

The shallowly convex, nearly oblong body is about 2.2 times as long as wide, and weakly convex at the posterior border. The moderately curved, strong dorsal process, inclined at 50 - 60° from the long axis of the body, is about 0.43× as long as the body. A strongly convex lateral expansion joins the proximal half of the dorsal process to the body.

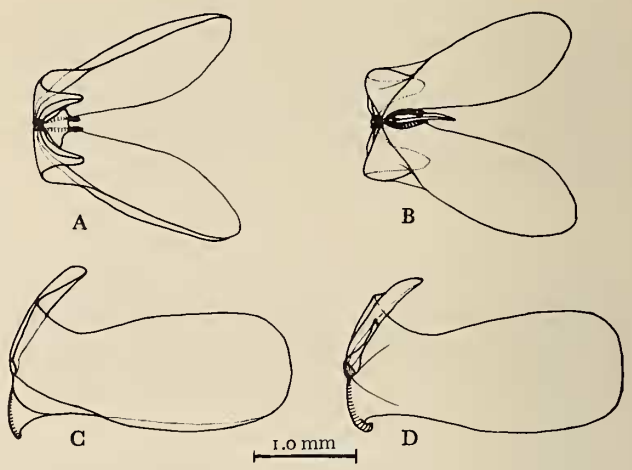

Figure 22

Dendronotus albus jaw
A. Dorsal view B. Ventral view C. Inside lateral view
D. Outside lateral view

The short masticatory process, inclined at about 80° from the long axis of the body and strongly curved distally, is joined to the body by a strong concave expansion.

The features that distinguish this jaw from that of the new species of *Dendronotus* are the shape of the body and the degree of divergence posteriorly of the 2 halves.

Radula

In the description of this species, a series of 15 radulae was examined and another 25 radulae were examined to check for additional variation. The resultant radula formula is 32 - 38 (6 - 8 · 1 · 6 - 8) (Figure 23). In all the specimens, the radula teeth were colorless. MacFarland (1966) reports a radula formula of 36 - 38 (7 - 9 · 1 · 7 - 9) and infers that all the median teeth are light yellow.

The bluntly pointed, denticulated cusp of the median tooth is relatively smaller than in the new species of *Dendronotus*; the width : height ratio varies from 1.8 - 2.0 (1.7 - 2.4) in the oldest teeth to 1.6 - 1.9 (1.1 - 1.9) in the newer teeth (Figure 6). Along each side of the median tooth cusp are 11 - 14 (7 - 17) denticles with the average being 13. These are small, relatively sharp, more or less regularly spaced, and usually increasing slightly in size towards the apex. In a very few animals, the denticles are missing or the edge of the cusp is very jagged from pieces being broken out.

The tall lateral teeth are relatively stout, and the inner ones bear long, curved cusps inclined about 20° toward the midline. In some of the innermost lateral teeth, the cusp is just slightly larger than the denticles, but more often it is about 2× longer. In the next 3 - 4 teeth, the cusp becomes progressively longer while teeth no. 5 (and no. 6) have a shorter spike-like cusp. In nos. 6 to 8, the cusp is usually missing.

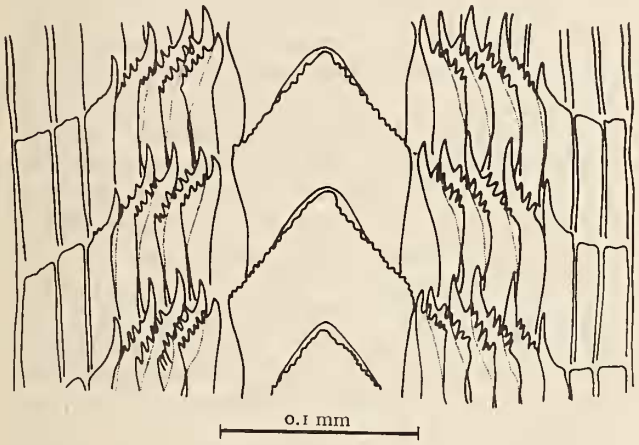

Figure 23

Dendronotus albus radula
Rows 25 and 26 in a radula with 40 rows of teeth

The proximal, lateral margin of the lateral tooth cusp bears from 3 - 8 relatively tall, stout, sharp-pointed denticles at nearly regular intervals. The 3 innermost laterals bear 4 - 6 (3 - 8) denticles while the next 2 bear 4 - 7 (3 - 9) denticles and no. 6, when it has denticles, carries 4 - 7 of them. The size and number of these denticles are rather distinct from those in the new species of *Dendronotus*.

Reproductive System

The thin hermaphrodite duct empties into a very wide, short, crescentic ampulla which suddenly narrows to a long spermoviduct (Figure 24). This divides to form a short, wrinkled oviduct and a very short proximal portion of the vas deferens. The prostate, comprised of 12 - 15 large, irregularly shaped alveoli arranged around the vas deferens as a concentric disc, is much smaller than that of the new species of *Dendronotus*. From it, the relatively short, quite narrow, weakly convoluted distal portion of the vas deferens arises. It tapers slightly immediately prior to entering the penis. The moderately long, narrow penis is tapered to a point.

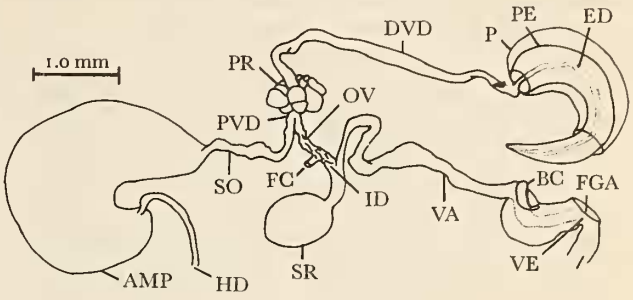

Figure 24

Reproductive system of *Dendronotus albus* (exploded view)
AMP = ampulla BC = bursa copulatrix
DVD = distal vas deferens ED = ejaculatory duct
FC = (to) fertilization chamber FGA = female genital aperture
FGM = (to) female gland mass HD = hermaphrodite duct
ID = insemination duct OV = oviduct P = preputium
PE = penis PR = prostate PVD = proximal vas deferens
SO = spermoviduct SR = seminal receptacle VA = vagina
VE = vestibule

The distal portion of the vagina passes through a very muscular mass, with unknown function, before it enters the vestibule. The long, flaccid, sac-like bursa copulatrix is located at the distal end of the vagina right over this mass. The rest of the vagina is moderately long and quite narrow, emptying finally into a stalked, spherical seminal receptacle. The insemination duct, arising from the base of the seminal receptacle, is very short, wrinkled, and transparent.

The major differences between *Dendronotus albus* and the new species are in the size and shape of the prostate, ampulla, vas deferens, and seminal receptacle.

Geographical Distribution

Dendronotus albus has been collected at a number of points around San Juan Island: Brown Island (10), Collins Cove (8), Lonesome Cove (3), and Edwards Reef (200). The only other area was Albert Head, Victoria, B. C. (2).

MacFarland (1966) collected *Dendronotus albus* at Monterey Bay. Lance (pers. comm.) reports collecting one specimen each at 3 places: the lower intertidal of Moss Beach (June 13, 1964); at 25 m in the *Macrocystis* sp. canopy near Scripps Canyon (July 24, 1967); and at 18 m in the *Macrocystis* sp. canopy south of the South Island, Islas Los Coronados, Mexico (June 22, 1961).

Ecology

From September, 1966 to January 1967 and during March, 1968, the animals were seen at depths of 20 - 30 m on rocky bottoms swept by strong currents most of the time. At Edwards Reef, the substratum consists of stones up to 18 inches across thickly scattered over a shell-gravel-sand base. These areas support dense, extensive hydroid populations of which *Thuiaria argentea* is often the most common species. Usually, the nudibranch was found clinging to the tip of the hydroid, and even careful searching failed to turn up more than a few animals crawling on the rocks. At Collins Cove where *T. argentea* is rare, the nudibranch was found on *Hydrallmania distans*. Laboratory observations suggest that *Dendronotus albus,* given a choice, will nearly always (95%) choose *T. argentea* over any other substratum.

Although no data are available on the mechanics of feeding, *Dendronotus albus* does eat *Thuiaria argentea,* normally confining itself to the distal portions of the stalk. Apparently it does not ingest the perisarc as this is not found in the fecal pellets.

The white egg masses are usually deposited at the tip of the branch of *Thuiaria argentea*, thus raising the eggs off the bottom and facilitating dispersal of the veligers as well as keeping the eggs clean. Many egg masses were deposited in the field and in the laboratory during October and November, 1966. No record of the number of eggs per capsule or the hatching time was kept. Copulation and well developed gonads were seen during March, 1968. The apparent reproductive isolation of the new species of *Dendronotus* and *D. albus* is mentioned below.

Both the nudibranch and its eggs are very conspicuous on the tips of the hydroids, making them easy to collect and probably easily seen by fishes. They have no obvious defense against predators, particularly fish, but the large number of mutilated specimens suggests that many are attacked and subsequently escape. Perhaps they have a distasteful epithelial secretion as do many other nudibranchs (Edmunds, 1966; Thompson, 1960b).

Dendronotus albus is able to swim quite well but its small size limits the absolute distance covered. Possibly, with the aid of currents, swimming may be an effective means of transport for the adults.

Dendronotus diversicolor Robilliard, spec. nov.

(Plate 64, Figures 35, 36; Text figures 4 - 6, 25 - 28)

Taxonomic Remarks

Marcus (1961, p. 34) includes under *Dendronotus frondosus* specimens that " . . . are white with orange-yellow points on the principal branches of the appendages," but these are probably *D. diversicolor.*

On the basis of MacFarland's (1966) description of *Dendronotus albus* it is difficult to separate *D. albus* from *D. diversicolor.* However, after examining many specimens, I was able to detect some obvious and some subtle internal and external characters that are consistently different in the two species. There is also some ecological evidence that attests to their uniqueness. These are indicated with a fuller description under the appropriate headings in both *D. albus* and *D. diversicolor.*

The most consistent morphological differences are in: the body size at maturity; the number of pairs of cerata; the body texture; the coloration and its pattern; the number and location of the hepatic diverticula; the denticulation of the radula; the overall shape of the jaws; and the proportions and shapes of the organs of the reproduction system. A thorough knowledge of the diagrams and descriptions of the above characters should allow the reader to distinguish one species from the other.

It could be argued, though with little validity, that the variation of the above listed characters is within the range of variation for a hermaphroditic gastropod. However, there are other factors which are not so easily reconciled.

The "ceratal cores" or hepatic diverticula extend into 3 - 5 pairs of cerata in *Dendronotus albus* and only into the anterior 2 pairs in *D. diversicolor.* It seems unlikely that those in the posterior 1 - 3 pairs should suddenly regress when the animal grows longer than about 3 cm. In fact, the larger *D. albus* (2.5 - 4.0 cm L) have diverticula in the 5th and 6th pairs of cerata as well. In the same vein, it seems unreasonable to postulate a sudden regression of the last 2 - 3 pairs of cerata as well as many of the smaller branches in the anterior pairs when the animal attains a length of about 3 cm.

Probably the most critical difference is the lack of sexual activity between the two species. No interspecific copulation was seen in the field or in the laboratory despite many observations of intraspecific copulation in the same animals. On many occasions, both species were placed together in an attempt to induce interspecific copulation, but with no success. Finally, *Dendronotus diversicolor* does not seem to develop mature gonads until it is more than about 4.0 cm L, whereas *D. albus* may be sexually mature and depositing eggs before it is 1.2 cm L. It might be argued that the larger animals are 2 years old and, having reproduced once, lived through the winter to breed again. Or, they may not have bred the first year; instead, they may have channeled the excess energy into growth and reproduced the second year. Miller (1962) suggests this may be true for *D. frondosus.*

Thompson (1964) reports that most hydroid-eaters pass through a number of generations in a year or at least live only one year. Preliminary observations in the field tend to support Thompson, at least for the small species of *Dendronotus,* including *D. albus* and *D. diversicolor.* It is for these reasons that I feel justified in establishing *D. diversicolor* as a new species.

The name has been chosen to draw attention to the variable pattern of pigments on the body and appendages, and the two color phases. The type locality is designated as Cantilever Pier, San Juan Island, Washington (lat. 48°32′48″ N; long. 123°00′18″ W). The collection of specimens from which the description is taken is deposited in the California Academy of Sciences, Invertebrate Type Series, Holotype no. 416. Paratypes are deposited at the Smithsonian Institution, and the Canadian National Museum (Ottawa).

Body Dimensions, Texture, and Apertures

The slender, limaciform body is relatively "delicate" for an animal of its size, and more laterally compressed than in the other species of *Dendronotus.* Because of the lack of cerata on the posterior third of the body, there appears to be a long tail tapering to a point. The high, rounded dorsum merges into the vertical sides with only the cerata to mark the junction between the two. In the present study the largest of 25 specimens was 7.3 cm L and the shortest was 1.5 cm L while most were 3.0 - 6.0 cm L. Representative sizes were: 5.2 cm L × 0.8 cm H × 0.4 cm W; 5.0 cm L × 0.7 cm H × 0.5 cm W; 1.9 cm L × 0.3 cm H × 0.2 cm W.

The small anal papilla, situated halfway between the first and second right cerata, is often covered with an opaque, dead-white pigment.

The genital apertures, which may not be conspicuous, are located about halfway up the right side just anterior to the base of the first right ceras.

The cardiac prominence may be only slightly raised, but more often, it is markedly protuberant. The surface of the body is very smooth; none of the specimens showed any sign of the papillation seen in other species.

Foot

The foot, about 10× as long as wide, is bluntly rounded in front and tapers in the posterior third to the sharply pointed tail. The sole is white in white animals, but is pale pink in lilac-colored animals.

The labile foot is able to cling most tenaciously to hydroid stems, making it nearly impossible to shake the animal loose. To be studied, it must be literally peeled off the stem. This degree of adhesion is extremely effective in allowing the animal to maintain its position despite the swift currents that normally sweep past it. The edges of the foot fold closely together when the animal swims.

Color

The translucent body may be either white or lilac (Plate 64, Figures 35 and 36). Fifteen animals were white while 10 were varying shades of lilac from cameo pink to pale violet. An opaque dead-white or a striking, opaque orange pigment, or both, may be found on the distal third of the main branches of the cerata, the posterior 1 or 2 crown papillae, the back of the rhinophore sheath, and the tips of the veil papillae.

In 15 white specimens, 13 had mostly white pigment (5 of these had a bit of orange at the very tip) and 2 had mostly orange pigment on the cerata. Each group also had a narrow orange or white band, respectively, proximal to the main pigmentation. Of the 10 lilac forms, 3 showed a predominance of white with only tiny caps of orange and the other 7 were basically orange with a narrow band of white proximal to the orange.

In all the specimens, there is an opaque dead-white, dorso-medial line extending from between the last pair of cerata to the tip of the tail.

Cerata

The 4, sometimes 5, pairs of tall, slender, sparsely branched cerata are arranged in a single row along either side of the dorsum with the interval between pairs decreasing very little. The height of the first 3 pairs of cerata is about equal while the 4th pair is about ½ to ⅔ as high. If present, the fifth pair is reduced to simple, short papillae.

The main branches are tall and slender, giving rise to few, relatively long, thin secondary branches, usually from the distal half of the stalk. The very few tertiary branches are short and almost transparent.

The branching pattern is "fan-shaped" (Figure 4a) with 3 branches in the first and second pairs of cerata, 2 (1 - 3) in pair no. 3, 2 (1 - 2) in pair no. 4, and 1 in pair no. 5. Where there are 3 branches, the nearly horizontal lateral stalk arises from the base of the ceras and, a short distance above that, the stalk splits to form 2 erect branches. In bifid cerata, the stalk divides at the base, giving rise to a lateral branch that is about ½ to ⅔ as tall as the medial one .

Extending into the medial 1, or more commonly 2, main branches of the first 2 pairs of cerata as well as into the rhinophore stalk are the hepatic diverticula. The first 2 pairs of diverticula arise from the anterior lobes of the liver and the last pair from the posterior lobe.

Rhinophore and Clavus

The tall, simple rhinophore bears a slender, unbranched lateral papilla originating between a third and halfway up the stalk and directed at about 60° from the horizontal. Usually, the lateral papilla is about $\frac{1}{4}$ the length of the stalk; in a few cases, it is reduced to a mere tubercle and, rarely, it is missing.

The conical, perfoliate clavus, in varying shades of white, cream, or pink, bears 16 - 21 deeply-cut leaves alternating in width. The narrow leaves are usually completely hidden by the wider ones.

Directed obliquely upward from the margin of the dilated, campanulate rhinophore sheath are 5 tall, thin, simply branched crown papillae. The postero-medial is about 2 to 3× longer. The shorter 3 are $\frac{1}{2}$ as tall as the rhinophore stalk.

Head, Lips, and Veil

The frontal margin of the indistinct veil bears 3 pairs of slender veil papillae that have a few short, slender branches arising from the distal half of the stalk and running nearly parallel to it. The medial pair, normally pointing straight ahead, is the longest. Pair no. 2, finger-like projections about a third to a sixth as long as no. 1, originate just ventro-lateral to the base of no. 1 and are curved ventro-medially. The lateral pair, at right angles to the long axis of the body, is about $\frac{3}{4}$ as long as no. 1.

There are 2 - 4 (2 - 8) simple, relatively long lip papillae located on the postero-lateral margin of the outer lips. The variation in numbers of papillae suggests that they are able to retract when disturbed; this has been noticed in a number of species.

Jaws

The thin, delicate jaws (Figure 25) are a transparent pale yellow, becoming more yellow at the hinge and masticatory process. In 1 preserved and 1 live specimens, I found buccal masses measuring 0.36 cm L × 0.19 cm W × 0.20 cm H (2.3 cm L animal); 0.4 cm L × 0.30 cm H (5.5 cm L; live).

The body is a convex, ovate mytiloid shape, widest in the posterior third, and about 1.8× longer than wide (Figure 5). The wide, curved, deeply grooved dorsal process, inclined at about 60° to the long axis of the body, is approximately 0.4× as long as the body. The lateral margin of the process flares outward and toward the hinge to form a strongly convex expansion between the dorsal process and the body. The short masticatory process is slightly (10°) inclined posteriorly.

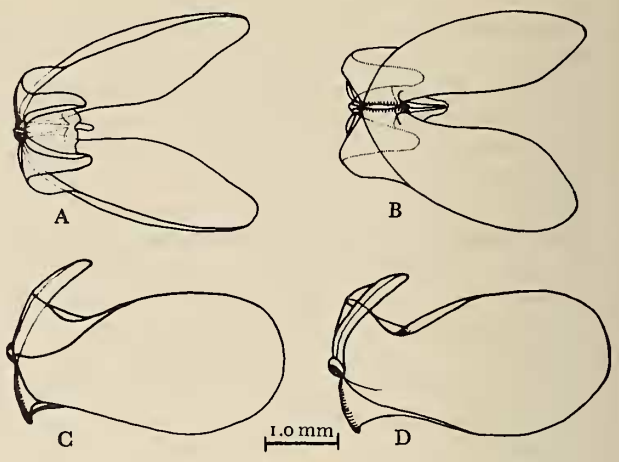

Figure 25

Dendronotus diversicolor jaw
A. Dorsal view B. Ventral view C. Inside lateral view
D. Outside lateral view

Radula

In this study, a sample of 11 animals had radula formulae of 33 - 38 (6 - 9 · 1 · 6 - 9). I found that only the anterior median teeth in 5 out of 11 animals were light yellow; the rest were colorless as in other species.

The strong, pointed cusp of the median tooth is 1.4 - 1.6 (1.3 - 1.8)× as wide as high (Figures 6, 26). Along either side are 13 - 17 (7 - 25) small, sometimes irregularly spaced denticles usually increasing in size towards the apex. In a few specimens, the edges were incon-

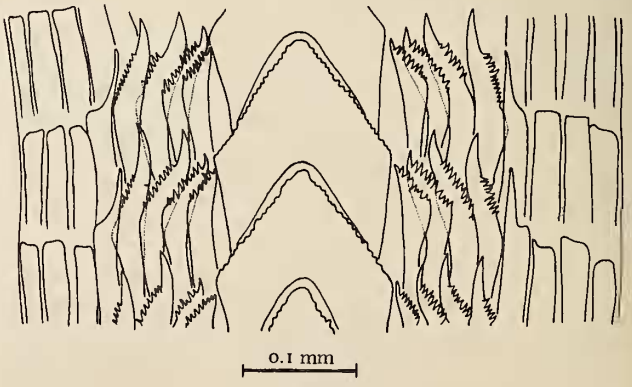

Figure 26

Dendronotus diversicolor radula
Rows 21 and 22 in a radula with 40 rows of teeth

spicuously serrulated, particularly on the anterior teeth, and in others these same teeth are quite jagged where pieces have been broken off.

The long, relatively wide lateral teeth bear elongate, slightly curved cusps inclined medially 10 - 20° from the long axis of the tooth. In the medial lateral tooth (no. 1) the cusp is about equal in size to the denticles, and in no. 2 it is about 2× longer than the denticles. Teeth no. 3 and no. 4 have the longest cusps, followed by no. 5 which has a long, thin, sharp cusp. The outermost 1 - 3 teeth lack a cusp entirely and no. 9 is reduced to a thin, narrow rudiment.

Borne on the lateral edge of the cusp are numerous relatively long, sharp denticles. On the innermost lateral tooth (no. 1) are 4 - 7 (4 - 12) denticles, 5 - 10 (4 - 13) on no. 2, 6 - 9 (4 - 14) on no. 3 and 5 - 11 (2 - 14) on no. 4. Only rarely does no. 5 have any denticles and then only a few.

Reproductive System

A dorsal view of the reproductive system *in situ* (Figure 27) shows the relationship of the genital apertures as well as giving some idea of the relative size that the "female gland mass" attains in a mature specimen.

The exploded system (Figure 28) indicates size and relationship of the components. The hermaphrodite duct suddenly widens to form a wide ampulla which is folded against itself for most of its length. The short, narrow spermoviduct bifurcates into a short, moderately wide proximal portion of the vas deferens, and wide, translucent, thin walled rugose oviduct.

The prostate, a flattened sphere, concentric with the vas deferens is comprised of many (30 or more) fairly large, irregularly shaped alveoli. Arising from the far side of the prostate is the very short, wide, weakly convoluted distal portion of the vas deferens. Just before entering the penis, it tapers to a narrow tube. The penis is a short, wide, nearly straight organ which tapers gradually to a blunt tip.

The vagina opens into the vestibule almost at the external orifice. The small spherical bursa copulatrix, supported on a long stalk, is located immediately proximally to the vaginal opening. The moderately long and narrow vagina terminates in a large, stalked, seminal receptacle resembling a squashed ovoid in shape. The short

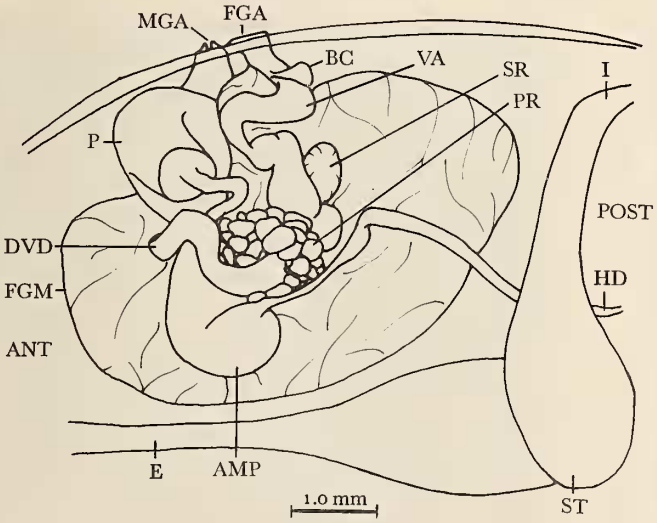

Figure 27

Reproductive system of *Dendronotus diversicolor*
In situ right dorso-lateral view to show the position of the genital apertures

AMP = ampulla ANT = anterior BC = bursa copulatrix
DVD = distal vas deferens E = esophagus
FGA = female genital aperture FGM = female gland mass
HD = hermaphrodite duct I = intestine
MGA = male genital aperture P = preputium
POST = posterior PR = prostate ST = stomach
SR = seminal receptacle VA = vagina

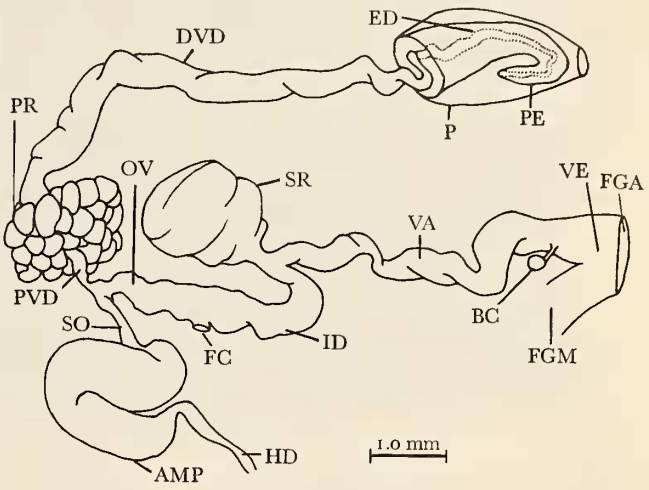

Figure 28

Reproductive system of *Dendronotus diversicolor* (exploded view)
AMP = ampulla BC = bursa copulatrix
DVD = distal vas deferens ED = ejaculatory duct
FC = (to) fertilization chamber FGA = female genital aperture
FGM = (to) female gland mass HD = hermaphrodite duct
ID = insemination duct OV = oviduct P = preputium
PE = penis PR = prostate PVD = proximal vas deferens
SO = spermoviduct SR = seminal receptacle VA = vagina
VE = vestibule

but wide, translucent, wrinkled insemination duct is confluent with the oviduct, the two emptying into the fertilization chamber.

Geographical Distribution

From July to December, 1966, I collected *Dendronotus diversicolor* at Point Caution (5), Brown Island (5), Collins Cove (8), Lonesome Cove (9), Eagle Point (8), all on San Juan Island, as well as at Peavine Pass (1) and Black Rock (1), both near Blakely Island in the San Juan Archipelago. Five animals were collected off the Victoria Breakwater in January, 1968.

Ecology

Adults were collected locally from July, 1966 to December, 1966, but none were seen from December, 1966 to March, 1967. They were collected again from May to August, 1967, and in March, 1968. All the animals were at 15 - 20 m on rock bottoms, thickly covered with numerous hydroid species and swept by strong currents. In the field, they were found on *Abietinaria greenei* (8), *Abietinaria* spp. (6), *Sertularella tricuspidata* (4), *Hydrallmania distans* (3), and unidentified hydroids (13). In the laboratory they prefer *Hydrallmania distans, Abietinaria greenei* and *A. amphora.*

The egg mass is much like that of *Dendronotus subramosus* in overall shape. In October, 1966, one white egg mass was seen in the field, while in the laboratory a lilac-colored animal deposited a lilac egg mass and 2 white animals laid white ones. Again in May, 1967, about 10 white egg masses were seen at Lonesome Cove and Eagle Point and 1 was laid in the laboratory. There was only 1 egg per capsule; the eggs took 8 - 13 days to hatch.

Against the dark background of rocks and hydroids, this nudibranch, perched on the distal third of the hydroid stem, is readily visible to a diver up to 20 feet away. The paucity of mutilated animals suggests that they have some effective, but as yet unknown, defense mechanism or that they are completely devoured, thus leaving no evidence of attack.

Like many *Dendronotus* species, *D. diversicolor* swims successfully when it is disturbed. So far, only mechanical stimuli have been effective in eliciting this response. As is true for many normally benthic invertebrates that occasionally swim, the swimming of *D. diversicolor* appears to be randomly rather than purposefully directed, with the currents determining the direction of the movement. Swimming may provide a means of escaping some predators, but it may also be important in the dispersal of the adults.

DISCUSSION

There are a number of reasons for the confusion over the validity of the species names in the genus *Dendronotus,* but the main one is the early, inadequate accounts which lack accurate and precise descriptions or diagrams, or both of the taxonomically important internal and external characters. For example, the descriptions by GMELIN (1791) of *Doris cervina* and by BERGH (1879) of *Dendronotus dalli* and *D. purpureus* leave no doubt that the animals are dendronotids, but the species designation is difficult. The reports of O'DONOGHUE (1921) were incomplete enough to lead ODHNER (1936, p. 1108) to say that "*D. rufus* ... cannot be separated (according to the description) [from *D. frondosus*]."

Because the important external characters like the rhinophores, cerata, lip and veil papillae, and color are very badly distorted after preservation, many of the earlier workers, especially BERGH, contented themselves with describing the internal anatomy. Unfortunately, they ignored the reproductive system, which has species-specific characters, and concentrated on the ganglia and nerves, digestive system, and circulatory system. All of these systems are remarkably similar throughout the genus. Most workers did include the radula, albeit often only briefly, thus giving their descriptions some limited usefulness.

Because most of the previous descriptions of *Dendronotus* have been based on one or a few specimens, there is no indication of the range of variation in the number, size, shape, *et cetera,* of the distinguishing characters. This "typological species concept" (MAYR, 1965) was no small hindrance when subsequent workers tried to decide if animals they had were forms of previously described species or a new species.

ODHNER (1934, pp. 229 - 230) outlined the criteria that he felt would make a species description more accurate and useful. To ODHNER's outline I would add only

Explanation of Plate 64

Figure 33: *Dendronotus subramosus* MACFARLAND, the most common color form found in the San Juan Islands × 1

Figure 34: *Dendronotus albus* MACFARLAND. The number of pairs of cerata (7) and the dorso-medial white line on the tail are sufficient to distinguish it from *D. diversicolor* × 2

Figure 35: *Dentronotus diversicolor* ROBILLIARD, spec. nov., white form. There are only 4 pairs of cerata (CE) × 1½

Figure 36: *Dendronotus diversicolor* ROBILLIARD, spec. nov., lilac form. The dorso-medial white line on the tail of this and the specimen in Figure 35 are not as distinct as usual × 1½

Figure 33

Figure 34

Figure 35

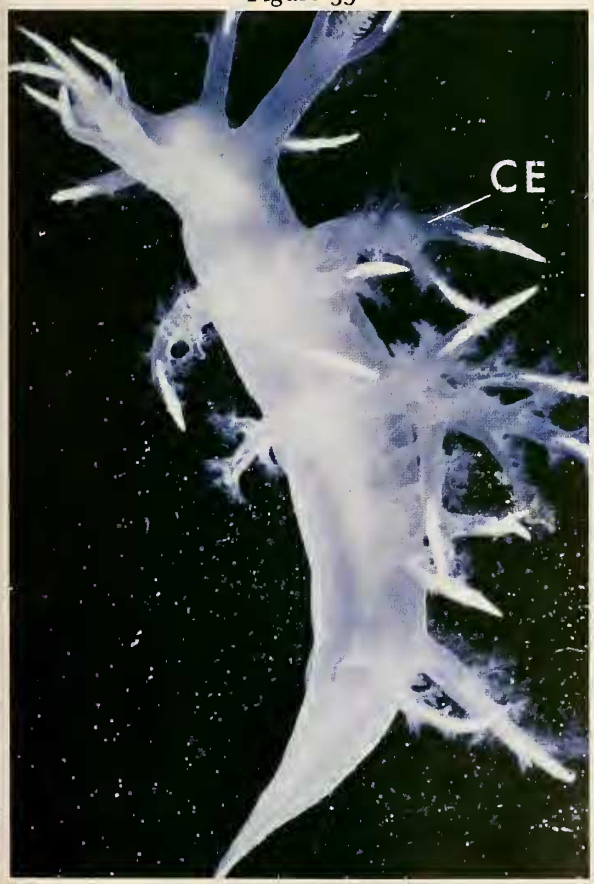

Figure 36

two essential criteria. The systematist should use a large series of animals to give some appreciation of the species' morphological variability and consistency. He should also have an understanding of the animal's ecology, particularly the feeding and reproductive behavior. The validity of a species of *Dendronotus* (or any nudibranch) established on the basis of the above criteria will probably stand the test of time.

A large sample of specimens provided the basis for separating *Dendronotus albus* from *D. diversicolor,* and *D. rufus* and *D. dalli* from *D. frondosus. Dendronotus albus* might have been considered a juvenile *D. diversicolor,* had not a long series of specimens pointed out the consistent differences as well as the limits of morphological variation in the two species. Odhner (1934, p. 19) states that there "... seems to be no reason for basing specific or varietal distinctions on the shape of the radula of this genus [*Dendronotus*]." However, when many more radulae are studied, limits of the variation in the teeth of any one species are recognized and species distinctions can be made.

Taxonomically, a knowledge of the reproductive biology of *Dendronotus* is the most important aspect of their ecology. This has been directly demonstrated in separating *Dendronotus albus* and *D. diversicolor.* The uniqueness of the other species has been determined partly on the basis of their reproductive isolation from each other.

There are definite peaks in reproductive activity, as indicated for each species, but egg masses and sexually mature animals can be found in small numbers at almost any time of the year. This plus the variation in size of animals collected at any one time suggests that reproduction occurs throughout the year.

Species of *Dendronotus,* like many nudibranchs, seem to be food specialists (Miller, 1961; Thompson, 1964), a feature that is useful in making field identifications. There are many other aspects of their ecology, discussed previously, which contribute to an understanding of the species and add more dimensions to the "multi-dimensional species" (Mayr, 1965).

As a last point, it seems curious that 7 of 9 species of *Dendronotus* should occur along the coast of the Northeast Pacific Ocean from Alaska to Baja California, that only 2 (possibly 3) species are found in the Atlantic Ocean, and that only 3 species are found in the Northwest Pacific Ocean. This may be an actual biological phenomenon with the Northeast Pacific being the center of evolution and radiation of the genus but it is more likely a reflection of the collection pressure. I would expect that more species will be found in the temperate waters of South America and Africa where relatively little collecting has so far been done.

Odhner (1936) lumped all the species described from the Atlantic under *Dendronotus frondosus* with the exception of *D. robustus.* However, *D. elegans* Verrill, 1880 is probably a specimen of *D. dalli.* There may be more species which have been incorrectly synonymized and which further work may reveal.

Further studies of the ecology as well as geographical distribution of the genus *Dendronotus* are needed to elucidate the problems concerning the evolution of the genus.

SUMMARY

Nine species of *Dendronotus* are described or redescribed: *Dendronotus frondosus* (Ascanius), *D. iris* Cooper, *D. robustus* Verrill, *D. dalli* Bergh, *D. rufus* O'Donoghue, *D. gracilis* Baba, *D. albus* MacFarland, *D. subramosus* MacFarland and *D. diversicolor,* spec. nov.

Dendronotus venustus MacFarland is considered a synonym of *D. frondosus. Dendronotus dalli* and *D. rufus* are taken out of synonymy with *D. frondosus* and established as valid species. *Dendronotus elegans* Verrill is considered a synonym of *D. dalli* rather than of *D. frondosus.*

The geographical distribution of the species of *Dendronotus* seems to be mainly limited to the north temperate and arctic waters. All species but *D. robustus* and *D. gracilis* are found in the Northeast Pacific Ocean. *Dendronotus robustus, D. frondosus* and possibly *D. dalli* are found in the Atlantic waters. Only *D. gracilis* has been found in south temperate waters (New Zealand).

Extensive descriptions of each of a large number of individuals are the basis of the species descriptions. External characters used, different interspecifically and consistent intraspecifically, were: the number, size, and branching pattern of the cerata, veil papillae, crown papillae, and lateral papillae; the number of lip papillae; the number of leaves in the clavus; the position of the anus and genital apertures; the size and shape of the body; the texture of the epidermis; the color and its patterns. Taxonomically important internal structures, described and figured, are the organs of the reproductive system; the radula; and the jaws. Each internal and external structure is defined and its function, if known, is discussed.

Of the 7 local species of *Dendronotus,* 5 appear to feed almost exclusively on various species of thecate hydroids. Of the other 2, *D. iris* feeds on the burrowing anthozoan, *Cerianthus* sp., while preliminary observations suggest that *D. rufus* feeds part of the time on scyphistomae. The food items of *D. robustus* are unknown.

Dendronotus iris is found on mud bottoms where there is little current action. *Dendronotus rufus* and *D. dalli* are usually in rocky areas with moderate currents while *D. albus, D. subramosus, D. frondosus,* and *D. diversicolor* inhabit rocky bottoms swept by swift currents.